International Society for Neuroethology

Newsletter
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International Society for Neuroethology
P.O. Box 1897
Lawrence, KS 66044, USA
Website: http://neuroethology.org/

Voice: +1-785-843-1235
(or 1-800-627-0629 Ext. 233)
Fax: +1-785-843-1274
E-mail: isn@allenpress.com

ISN Officers

Next ISN Congress: Salamanca, Spain, 4-7 August 2010. Local organizer: Alberto Ferrús, Instituto Cajal, C.S.I.C., Avenida Dr. Arce 37, E-28002 Madrid, Spain. Tel: +34-1-585-4739; Fax: +34-1-585-4754; aferrus@cajal.csic.es

This Issue Includes

Letter from the President

Martin Heisenberg
Theodor Boveri Institut (Biozentrum), Lehrstuhl für Genetik und Neurobiologie, Universität Würzburg

Dear ISN Members:

On July 19 the Executive Committee of the ISN convened in Cambridge, MA for its annual meeting. Several new initiatives were launched. It is planned for instance (a) to support short-

term visits of young scientists for learning new techniques or for doing a particular experiment in an other laboratory, (b) to offer special awards to scientist from emerging countries for participating at the International Congress of Neuroethology, and (c) to sponsor each year a small conference on a specialized topic of Neuroethology. These programs will be announced in the Newsletter as soon as their financial foundation is secured. Activities of the society in non-congress years remain a major concern. This year the society funds 8 Heiligenberg student travel awards. Preparations for the next congress in Salamanca in two years are well on their way. Please note already the date: August 4-7, 2010.

While in full blossom regarding its science, the society is handicapped by its difficult name: Neuroethology. Historically, this term united a small group of scientists around Ted Bullock, Franz Huber and a few others who considered the neurobiology of natural behaviour the most exciting part of functional brain science. The success of this approach gave the tri-annual congresses their special excitement and enthusiasm. I would like to emphasize that today the society is open to any research areas addressing the relation between brain and behaviour. Systems Neurobiology, the newest addition to the behavioural neurosciences would be as welcome as had been in the past, for instance, Behavioural Endocrinology or Cognition research.

If you want to support Neuroethology via the ISN beyond your dues, if you want the ISN to be the market place of your science and the ICN the conference where you meet your friends, please, help recruit new members. We will have a flyer with a membership application form for distribution at summer schools, workshops or conferences. You can obtain it from Linda Hardwick <lhardwick@allenpress.com>.

Thank you.

Your President

The Week the International Society for Neuroethology was Born

Goerge Pollak (gpollak@mail.utexas.edu) University of Texas at Austin, School of Biological Sciences

It was late summer of 1981 when it all started, at a meeting titled *Advances in Vertebrate Neuroethology* that was organized by Peter Ewert in Kassel, Germany. The meeting was international, but it was not at all clear that any of scientists from the U.S. would attend, since it was the summer of 1981 when air controllers went on strike and Ronald Reagan fired them all. But somehow we all made it to Kassel, and had not only a truly exceptional meeting but gave birth to the International Society for Neuroethology. I was one of those who made it to the meeting and here I recall, as best I can after more than a quarter of a century has passed, the events that eventually culminated in the formation of the ISN.

The meeting focused on vertebrate neuroethology, and was small (about 70 participants), intimate and the atmosphere was simply bursting with the excitement of new discoveries. The status of the scientific careers of the people who attended ranged from the established giants, Ted Bullock, Mark Konishi, Walter Heiligenberg, Peter Marler, Bob Capranica and Nobuo Suga, to younger scientists who had already made significant contributions but whose careers subsequently blossomed into some of the most distinguished in science. Some of the younger scientists were Peter Narins, Ed Rolls, Joe Eggermont, Russ Fernald, Uli Schnitzler, Henning Scheich, Gunther Ehret, Carl Hopkins, David Crews, Giacomo Rizzolatti, Jim Simmons and Andrea Megala to mention just a few. What I remember so vividly is the excitement, exuberance and the collegiality. It was simply an exciting time and a wonderful meeting.

Neuroethology was a new field but already had put its firm imprint on science with the success of several model systems. Walter Heiligenberg and his colleagues were dissecting, with consummate skill, the circuitry and processing that underlie the jamming avoidance response in weakly electric fish, while Bob Capranica and his students were showing the species-specific peripheral adaptations in the anuran auditory system and that frequencies in their advertisement calls were uniquely combined as mating call detectors in the forebrain. Nobuo Suga's studies were revealing the exquisite functional organization of the mustache bat's auditory cortex, and the discovery of the space map in the owl's tectum, by Mark Konishi and Eric Knudsen, galvanized the neuroscience community. These seminal discoveries were scientific triumphs and created entire fields that continue to reveal the workings of the nervous system to this day.

If we had just heard updates on the owls, frogs, bats and fish, the meeting would have been successful. But I remember several talks that were prescient. Mark Konishi announced, in his characteristic understated manner, that one of his graduate students, Dan Margoliash, had found neurons in the forebrain of song birds that responded selectively to the bird's own song! The buzz was palpable and Mark told us about the findings in an informal talk. Joe Eggermont's talk, on coding in the frog midbrain, described the first spectrotemporal receptive fields generated by spike-triggered averaging. I was sitting next to Russ Fernald who turned to me and remarked, "that is going to be important". Russ, I am sure, does not remember that moment, but I do, and he was spot on. David Perrett presented the studies he conducted with Ed Rolls on recordings from neurons in the inferior temporal cortex of monkeys that responded selectively to faces or facial features, and the implications of those findings for prosopagnosia. I was absolutely speechless! These were not the only outstanding talks, but the ones I recall after more than 25 years have passed. I apologize to those whose talks I have not mentioned

Personalities also colored the meeting, but with a positive influence and sometimes in a most entertaining way. I met David Perrett for the first time, and he was garbed in Punk, leopard pants and multicolored hair, that stood out like a flashing neon light against the conservative attire of his mentor, Ed Rolls, and the more drab clothing that the rest of us routinely wore. Walter, of course, always appeared in his white turtleneck sweater. Who could even imagine Walter without his white turtleneck. He was simply a dynamo. He was everywhere, interested in everything. Walter was not only a stellar scientist but also an inspiring and wonderful person who touched people's lives. I miss Walter very much, as does everyone who knew him. I also met Franz Huber for the first time, and I remember it well. Although the focus of the meeting was on vertebrate neuroethology, Ted and Peter invited Franz to give a talk that I can still hear rumbling in my memory banks. Indeed, I can still "see" Franz on the podium, telling us, with his commanding presence and in his thundering style, that the basic mode of processing in invertebrates is the same as it is in vertebrates, ticking off each feature, one at a time, while maintaining eye contact with the audience and somehow making you think he was focusing on you. It was a quintessential "Huber" talk and I'll never forget it! Franz is now retired, and he hasn't changed a bit! I had dinner with Franz in early May and he is still the embodiment of energy and dynamism. I feel privileged to have him as a friend.

The meeting brought a mixture of people together at a time when numerous model systems, both vertebrate and invertebrate, had proved their worth and when new findings, each more surprising than the next, were occurring at an accelerating rate. All of these ingredients came together in one place at one time at Kassel, and what became apparent was that neuroethology had matured to a stage where it needed its own identity and its own organization. But it is one thing to want an organization and another to bring all the parts together and actually make it happen. We needed someone with the stature, experience, organizational skills, political acumen and desire to transform an idea into a reality. That person was Ted Bullock. Ted was the main organizer and the driving force behind the creation of the Society, and he did it out of love for his field. Because of Ted's efforts, the International Society for Neuroethology was formed during the final session of the meeting. Subsequently, Mark Konishi was elected as our first president and the rest is history.

Professor
Goerge Pollak
University of Texas
at Austin, School of
Biological Sciences

Reflections on the Academic Career of Sten Grillner: a Co-Awardee of the Inaugural 2008 Kavli Prize for Neuroscience

Douglas G. Stuart (dgstuart@u.arizona.edu). Department of Physiology, University of Arizona, Tucson, AZ 85724-5051, USA

Hans Hultborn (h.hultborn@mfi.ku.dk) Department of Neuroscience and Pharmacology, University of Copenhagen, DK-2200 Copenhagen N., Denmark

The Kavli Foundation was established in December 2000 by its founder and benefactor, Fred Kavli, a prominent Norwegian-born California business leader and philanthropist, the goal being to promote research in astrophysics, nanotechnology, and neuroscience in the United States, Europe and Asia. This year, the Foundation, in collaboration with the Norwegian Academy of Science and Letters (NASL) and the Norwegian Ministry of Education, initiated the biennial awarding of prizes in these three areas. For neuroscience, the 2008 co-awardees are Pasco Rakic (1933-), Thomas Jessell (1951-), and our close friend and colleague, Sten Grillner (1941-; Fig. 1), who is a founding member (1981) of the International Society of Neuroethology and a Council Member in 1996-2000.

Fig. 1. A recent photograph of Sten Grillner that was taken by his wife. Lena Grillner is a distinguished academician and clinician in her own right as Professor and Chair, Clinical Microbiology and Group Leader of a microbiology research unit (www.ki.se/labmed/gkgroup/lenagweb.htm), Karolinska Institute.

The NASL announcement of this prize states that the selection of these three neuroscientists was based on their " … discoveries on the developmental and functional logic of neuronal circuits," with Sten's contribution involving the elucidation of " … basic principles of neural circuit organization and function that control vertebrate locomotion using lamprey as a model system" (for further details see http://www.kavliprize.no/).

In association with announcement of the prize, Glover (2008) has provided an excellent account of the three awardees' research contributions. His report includes Sten's work on the lamprey and other neuroscientific issues, and his overall contributions to the study of locomotion, which have been at the forefront since the early 1970s (see, e.g., Orlovsky et al., 1999; Stuart, 2007; Grillner et al., 2008). In this article, we provide some very informal and personal reflections on other aspects of Sten's academic career; with an emphasis on our own separate interactions with him over the years, and his research mentoring/collaborating and service contributions.

Interactions with Sten

Recall by DGS. I first met Sten in a pub in Munich in the summer of 1971 while we were participating in the XXVth International Congress of Physiological Sciences. Fig. 2 shows how he looked in those days!

Fig. 2. A photograph of Sten Grillner that was taken by Tomas Palm in the Department of Physiology, University of Göteborg in the mid- to late 1960s. Tomas was the department's photographer at that time.

Sten had recently completed several months of postdoctoral research in Moscow, USSR before returning to his academic unit in the Department of Physiology, University of Göteborg, Göteborg, Sweden. I was on the way to the same unit to work for 7 months with its head, Anders Lundberg (1920-) and his long-standing colleague, Elzbieta Jankowska (1930-). In my first discussion with Sten, which was most enjoyable and high-spirited, Sten summarized his experiences working in Moscow on the neural control of locomotion with Mark Shik (1934-) and Grigori Orlovsky (1932-) while I brought to the table new data on the neural control implications of high-speed locomotion in Arizona cats. Subsequently, we gave seminars on these topics in Lundberg's unit. Sten's seminar made a lasting impression on me because in addition to presenting the locomotion research he had undertaken in Moscow, he summarized the organization and operation of several theoretical and experimental groups at the Institute of Problems of Information Transmission. Sten explained how these groups featured interdisciplinary interactions between physical and life scientists, invertebrate and vertebrate biologists, and basic and clinical scientists. Subsequently, he developed such a group in Stockholm, Sweden, with much ongoing success and longevity.

When Sten and I were in Göteborg in 1971-72, we continued our animated and lengthy discussions, with an emphasis on an intriguing article Sten was preparing on a neuromechanical aspect of motor control and on our different approaches to reviews that we each was beginning to write on the neural control of locomotion. Sten's review (1975) was a tour-de-force. It featured virtually equal weight given to work undertaken on non-mammalian and mammalian vertebrates, key findings on invertebrates, and it had a strong emphasis on pattern-generation circuitry. During its early (1971-72) preparation, I was in awe of Sten's focused, time-consuming concentration on mastering not only invertebrate and non-mammalian neurobiology in particular, but also the all-round biology of these species. Clearly he is a worthy founding member of the International Society of Neuroethology!

Subsequent to our 1971-72 discussions in Göteborg, we interacted, along with Paul Stein (1943-) and at different times with Hans Forssberg (1949-), Richard Herman (1928-) and Allen Selverston (1936-), on the organization of several symposia, the goal being to stimulate integrative and comparative work on the neural control of locomotion. These symposia (Philadelphia, 1975; Stockholm, 1985; Tucson, 1995), Sten's most recent one (Stockholm, 2006), organized again with Paul Stein, and also Ole Kiehn (1958-), Abdeljabbar El Manira (1965-), and Serge Rossignol (1942-), and the follow-up symposium publications have not only advanced the field but most importantly they have stimulated international cooperation and collegiality. Throughout these interactions, I was continually in awe of the breadth and depth of Sten's grasp of the control of locomotion and his intense interest and genuine respect for the work of others. These sentiments are shared widely throughout the international movement neuroscience community.

Recall of HH. I was recruited with some personal uncertainty into Anders Lundberg's neurophysiology unit in 1965 following the oral exam in medical physiology. But after a year in this unit there seemed no alternative to a full commitment to neurophysiology! It was not just the subject, but also the spirit and camaraderie in Lundberg's unit. There were also several slightly senior colleagues who captivated me. Sten was at the forefront among them, only a few years older than me, but already far ahead in his work for a PhD thesis on the supraspinal control of gamma motoneurons (Grillner 1969). Sten and

other young Swedish researchers served as role models together with innumerable international neuroscientists attracted to Lundberg's unit (see Stuart and Hultborn 2008). Toshinori Hongo (1932-) was one of them - and a most important one as a senior and stimulating collaborator for Sten during his thesis work. As part of his work, Sten investigated the reflex activation of gamma motoneurons in spinal cats by stimulation of high-threshold limb afferents following administration of DOPA (3,4-dihydroxy-L-phenylalanine) (Grillner et al., 1967). Just previously, Lundberg and coworkers had implicated these pathways in activating the spinal program for locomotion by (see Stuart and Hultborn, 2008). Sten also noted that DOPA administration could occasionally evoke locomotor activity in his spinal-cat experiments. After finishing his thesis, Sten elected to focus on the spinal control of locomotion. In 1971, he spent valuable and productive time with Mark Shik and Grigori Orlovsky at the Institute of Problems of Information Transmission, where they worked on locomotion evoked in decerebrate cats by stimulation of the mesencephalic locomotor center. Shortly after returning to Göteborg, he recruited a student, Hans Forssberg (1949-). Together, they discovered that the alpha-adrenergic agonist, clonidine, made it possible for acutely transected spinal cats to walk on a treadmill. Subsequently Sten worked on the recovery of locomotion following chronic spinal transections in kittens – but now without pharmacological interventions. This was done together with a Canadian postdoctoral researcher, Serge Rossignol (1942-), who arrived in 1973. Even though Sten continued work on cat preparations with great success for several years, he decided in the early 1970s to search for a simpler preparation that could offer better possibilities for an analysis of the underlying network and cellular properties. Together with Claude Perret (1942-) from France and Peter Zangger (1945-) from Switzerland, Sten demonstrated a spinal locomotor CPG in the deafferented, curarized dogfish shark, catching this latter on the Swedish west coast at Kristineberg. Peter Wallén (1950-), a biology MS student, soon joined in this effort. He had been recruited by Sten to join his Göteborg laboratory in 1974. They are still working closely together in Stockholm, now 34 years later!

Glover (2008) has emphasized the importance of Sten's initial spinal cat and dogfish shark experiments. They revealed that across vertebrate species, the spinal cord had the intrinsic neuronal circuitry to generate locomotion, with powerful support from sensory feedback. At that time, I had just returned from my own postdoctoral training in Japan, and I still remember with great vividness and affection our regular lunches at “Restaurant Prague” where Sivert Lindström (1942-) and I were privileged to hear first-hand about the rapid progress being made by Sten and his emerging talented group.

When Sten's laboratory moved to Stockholm in 1975, his non-mammalian research focus turned from the spinal dogfish to the lamprey, an enlightened strategic move that continues to advance network neurobiology, both experimentally and computationally (see Glover, 2008). His lamprey research has resulted in many well-deserved accolades including now a Kavli Prize.

Looking back, my own all-round academic interactions with Sten and his coworkers during his Göteborg years were indeed most exciting and helpful. After Sten’s move to Stockholm, I continued to profit from my interactions with him during frequent visits to Stockholm for courses, seminars, and conferences. My most recent visit was in June 2008 for the Nobel Symposium on “Genes, Brain and Behavior.” Interestingly, all three of the Kavli prizewinners in neuroscience were present!

Sten's extensive research mentoring and collaborations

Since 1973, Sten has supervised the PhD research of 22 neuroscientists, mentored 46 postdoctoral trainees, and collaborated with 14 established scientists in his laboratory that was first located in Lundberg's Göteborg unit (1969-75), then his own research unit in the Department of Physiology III, Karolinska Institute (1975-86) and finally, this institute's Nobel Institute for Neurophysiology (1987-) and Department of Neuroscience (1993-).

There are three remarkable features to Sten's research mentoring and collaborating. First, they reflect Sten's transnationalism. His trainees and collaborators were born in 18 countries, including: Australia, Canada, China, France, Great Britain, Germany, Italy, Japan, Lithuania, Poland, Russia (USSR), Spain, Sweden, Switzerland, The Netherlands, Ukraine, USA, and Venezuela. Second, the group includes neuroscientists who have subsequently worked on a wide variety of invertebrate and vertebrate species and research topics. Third, in terms of the quality of their contributions, the group is a virtual "who's who" of interdisciplinary international movement neuroscience! Clearly, Sten's research mentoring and collaborating are a major feature of his academic career.

Sten's remarkable service record

Sten's CV documents his election to several prestigious academies of science and letters in his native Sweden and abroad. He has also been honored by the reception of several similarly distinguished international awards, including now a Kavli Prize in Neuroscience. In this brief tribute we prefer to focus, however, on what Sten has accomplished for neuroscience in general, and movement neuroscience in particular.

Over the years, Sten has been a conscientious and painstaking editor for 14 top-tier refereed journals and he has been similarly thorough on 29 "commissions of trust," including advisory boards, councils, evaluation panels and membership committees. These assignments have been for 12 international groups and 11 individual countries including Belgium, China, Germany, Finland, France, Japan, Norway, Spain, Sweden, Switzerland, and USA. Also, Sten has led or helped the planning of 26 international symposia and congresses (4 were mentioned above), including ones in the Czech Republic and Italy in addition to those in countries mentioned above. In our opinion, it is remarkable that he has been able to accomplish all of this while advancing locomotion research in his own research unit.

Summary thoughts

Many of our colleagues have had the good fortune to begin their research careers in an optimal environment and with out-

standing research mentors like those enjoyed by Sten at the University of Göteborg. Few indeed have then exploited this advantage to the extent that Sten has. This ever-continuing desire to advance neurobiology is a great credit to all who have influenced Sten along the way and most significantly to him, himself. Sten is indeed the quintessence of excellence among those undertaking research in neuroethology and its allied disciplines.

Acknowledgement: We thank Paul Stein, who has interacted closely with Sten over the years, for editing the penultimate version of this article.

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A Breakthrough in Brain-Machine Interface

Lise Johnson (johnson.lise@gmail.com)
Department of Physiology, The University of Arizona

The June 19, issue of *Nature*, has an exciting and newsworthy paper form the laboratory of Andy Schwartz at Pittsburgh University (Velliste et al., 2008 "Cortical control of a prosthetic arm for self-feeding." Nature 453:1098-1101). The story was widely picked up by the popular press, which has enthusiastically promised new hope for paralyzed patients. The excitement is not unwarranted. In a *News and Views* article in the same issue (1), John Kalaska of the University of Montreal said the research "represents the current state of the art in the development of neuroprosthetic controllers for complex arm-like robots that could one day, in principle, help patients perform many everyday tasks such as eating, drinking from a glass or using a tool."

Prior to this study, cortical control of simple robotic devices, or the cursor on a computer screen, had been demonstrated in both humans and animal models (2,3,4). However, in these experiments the subjects did not interact with the physical environment. In this study the connection between intention and action was made by teaching monkeys to perform a natural behavior (feeding) using a neuroprosthetic arm.

Two monkeys were pre-trained to control a human-like robotic arm with a joystick. Arrays of intracortical microelectrodes were implanted in the primary motor cortices of the monkeys. For each monkey, single and multi-unit spiking activity recorded from these electrodes comprised the input to a (relatively) simple population vector algorithm. The algorithm transformed the neural signal into a control signal for the robotic arm in real time. Using visual feedback, the monkeys were then trained to generate neural patterns that produced desired movements of the arm. In this way the monkey continuously and smoothly controlled the prosthetic, which he used to reach for a food target, to grip the target between two "fingers", and then to bring the food back to his mouth. The monkey exercised precise control over the robotic limb, even executing curved trajectories when necessary and rapidly changing trajectories when the target was moved. Although this task was significantly more difficult than the tasks performed in previous studies, both of the monkeys accomplished this feat rather effectively, with a combined success rate of 61%. Videos of the animals feeding themselves with this method are sure to impress the viewer and are available as part of the supplementary material for the original article.

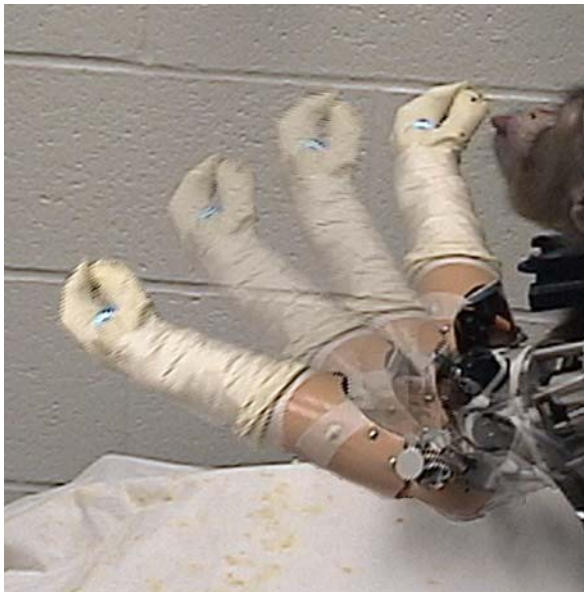

Fig. 1. The robot arm bringing a morsel of food to the monkey's mouth.

The monkeys also demonstrated some interesting behaviors which were not predicted and which could not have been observed without physical interaction with the environment. For

example, the monkey learned trough the course of the experiment to gradually open the gripper fingers on the return path to his mouth in order to unload the reward more quickly. Interestingly, the monkey also sometimes moved the arm to lick the gripper fingers or to push the food into his mouth. This adaptive behavior suggests that the monkey was using the artificial limb as a surrogate for his own arm.

These results are an impressive demonstration of the capabilities of a brain-machine interface. We are now one step closer to the development of a dexterous artificial limb, which is controlled by the central nervous system, and which restores a high degree of function to the user. However, although it offers us a foretaste of what may be possible someday; a neuroprosthetic of that sort is not yet a reality.

In an interview with Jeffrey Brown of PBS's *The News Hour*, the senior author of the paper, Andrew Schwartz, identified what he considers to be the two developments that are necessary prerequisites to a clinical device; chronically implantable electrodes and a better understanding of how the brain encodes movements of the wrist and hand. We would add to that list the integration of sensory feedback, without which the user is unable to judge the force with which an object needs to be grasped. Substantial as these obstacles may seem, they are by no means insuperable and a concerted effort by multiple research groups is underway to address each of these issues. For example, the author of this article is experimenting with the probabilistic control of functional electrical stimulation to elicit complex, multiple joint movements. The objective of the study, which is directed by Dr. Andrew Fuglevand at the University of Arizona, is to find a mapping between kinematic parameters and muscle activity so that cortically generated directional signals, like those used by Velliste et al., can be used to control the arm and hand instead of a robot. This approach is appealing not only because it reduces the amount of necessary hardware, but because the cortical signals can operate on their natural substrate. This is an important point because, as Velliste et al. have suggested, an arm that moves more naturally is easier to control.

This motor control group has been working for decades to accomplish this extraordinary feat which is both scientifically interesting and directly applicable to medical rehabilitation. To see footage with the monkeys and the robot in interaction please visit the following website:
http://motorlab.neurobio.pitt.edu/multimedia.php

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The Pluses and Minuses of Neuromodulation

Ron Harris-Warrick and Bruce Johnson
Department of Neurobiology and Behavior
Cornell University, Ithaca, NY 14853, USA

Flexibility is a key feature of all behaviors generated by animals: they must be able to modify their behavior to suit the immediate demands that face them. Thus, there is strong evolutionary drive to develop mechanisms to reliably alter the output of motor networks that drive simple rhythmic behaviors such as locomotion and mastication. Neuroethologists have looked for many years at these mechanisms, which include the actions of descending commands from higher brain areas onto the motor networks (evoked, for example, by seeing a predator approaching), the effects of sensory feedback (evoked, for example by tripping over a log), and the slower and more tonic effects of neuromodulators. In this essay, we will focus on how neuromodulators reconfigure neural networks for behavior.

Neuromodulators, such as amines and peptides, typically act slowly (over hundreds of msec to minutes) to alter the function of a network for a more prolonged period of time. In many cases, they appear to be essential to enable the network to function at all: in the absence of modulatory inputs, many networks fall silent and the behavior cannot be elicited. Modulators also serve to modify the output of the network, providing a tonic "bias" to the network output for the period of the modulator action. These actions are mediated by direct effects on two components of the network: the strengths of the synaptic connections that make up the "wiring diagram" of the network, and the intrinsic firing properties of the neurons that determine their baseline firing pattern (silent, tonic, bursting) and their interpretation of synaptic inputs (post-inhibitory rebound, spike frequency, etc.).

While modulation appears to be essential for the normal function and plasticity of many neural networks, there can be too much of a good thing: if the network is "overmodulated", it could fall apart and become non-functional. For example, if the strengths of the synapses or the intrinsic properties of the network neurons are changed too much, the network may not be capable of generating the output that drives appropriate muscle contractions for a coordinated movement. Thus, along with studying how neuromodulators can change the network's properties and its output, we now have to start looking at the constraints on those changes that keep the modulation within bounds where the network output is still functional and adaptive.

Based on our detailed studies of amine modulation in the crustacean pyloric network of the stomatogastric ganglion, we hypothesize that one way that this stability in the face of neuromodulation can occur is by a complex set of partially opposing effects of the neuromodulator. The modulator thus activates some mechanisms to change the network function in a particular direction, while simultaneously activating opposing mechanisms to constrain the change so that it is still within the functional range of the network. To take a simple parallel of a train on a track that moves from one station to another, an engineer would build an accelerator (the engine) to move the train towards the station, and a brake to stop it when it gets there and prevent it from overshooting its goal. Thus, in studying modulatory actions on behavioral networks, we should look for both accelerators and brakes in their actions to stabilize the network in the new, modulated state. In this essay, we will present some evidence to support this hypothesis by looking at how dopamine modifies the strength of synapses in the pyloric network in the spiny lobster, *Panulirus interruptus* (Fig. 1).

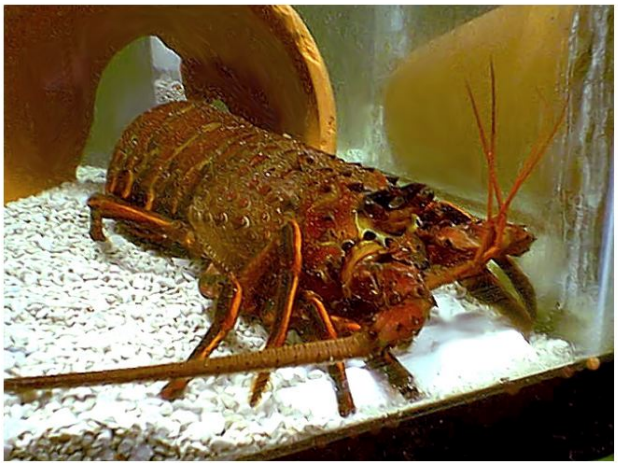

Fig. 1: Panulirus interruptus

The crustacean pyloric network

The stomatogastric ganglion (STG) is a tiny bag of about 30 neurons that control rhythmic movement of the foregut of crustaceans such as lobsters and crabs[1]. These 30 neurons comprise several neural networks that drive different aspects of the foregut rhythmic behaviors. The pyloric network, which contains only 14 neurons in 6 major classes, controls the rhythmic pumping and filtering movements of the pylorus. They communicate by electrical coupling, and both spike-evoked and graded chemical inhibitory synaptic transmission. Graded release occurs as a continuous function of voltage, with a threshold near or below the lowest voltage swing of the neuron's oscillations. Thus the neuron is releasing transmitter most of the time, but more when it is depolarized.

The behavior generated by the pyloric network is a triphasic rhythmic series of muscle contractions in the posterior region of the foregut, mixing finely ground food particles with digestive enzymes and moving it into the midgut for adsorption. The great experimental advantage of this very simple behavior is that it can be elicited in the dish by the isolated stomatogastric nervous system, which consists of the STG and its nerves running to the pyloric muscles, connected to three higher ganglia that provide modulatory inputs. These modulatory inputs are essential to activate the pyloric rhythm: when they are blocked, the pyloric rhythm slows and often stops. Bath application of a number of amines and peptides, probably mimicking their paracrine hormonal action in the ganglion, can reactivate the pyloric motor pattern, but the details of the pattern are different for different modulators. Further, if the motor pattern is already running with intact modulatory input from the higher ganglia, addition of a single modulator can modify the motor pattern in fairly stereotyped ways..

For the past 25 years our lab has engaged in detailed studies of the cellular and biophysical mechanisms by which three monoamines, dopamine, serotonin and octopamine, reconfigure the pyloric ganglion in *P. interruptus*.
(Fig. 1)[2,3]. Each of these monoamines can elicit a unique motor pattern from the quiescent pyloric network in the isolated STG, and can elicit unique and reproducible changes in the ongoing network with descending modulatory inputs intact (Fig. 2).

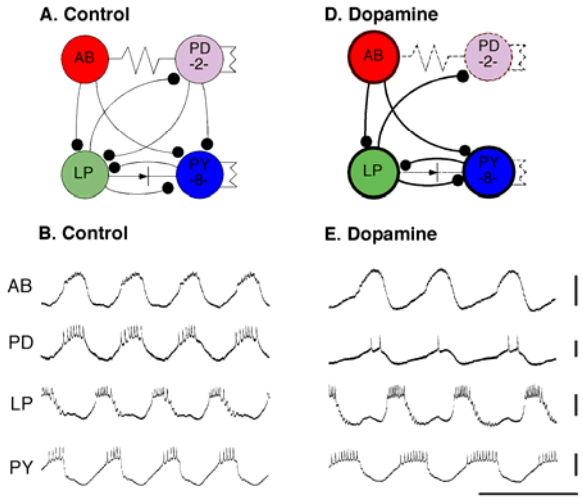

Fig. 2: Effects of dopamine on the pyloric motor pattern. A: Control motor pattern with intact modulatory inputs from other ganglia, and simplified wiring diagram of the neurons. B: Change in the pattern after adding 10^{-4} M dopamine. Strengthened synapses shown with thick lines, while weakened ones are shown with dotted lines.

Due to the simplicity of the network, we can isolate each of the 14 neurons from all synaptic input and study how the amine modifies that isolated neuron, to determine its direct effects. We can also isolate two neurons with their synaptic connection intact, and study how the amine modifies the strength of that synapse. We found that dopamine, serotonin and octopamine each directly modulate nearly all of the pyloric neuron cell types, but with a variety of different effects on different neurons for a single modulator, ranging from simple inhibition to evoking rhythmic bursting. Similarly, the amines

increase or decrease the strength of nearly all the synapses in the network, effectively "rewiring" it for a new behavior. Detailed voltage clamp and calcium imaging studies exposed a remarkably complex set of modulatory effects of each amine. For example, DA affects each neuron and each synapse in the network. For each neuron, it modifies the properties of multiple ionic conductances. For each synapse, it modifies both pre-synaptic release of transmitter and the post-synaptic response to that transmitter. Among all these effects are many examples of DA having opposing actions on a single cell or synapse, such that the majority effects are constrained by the opposing minority effects to rein in the amount of modulation of the cell or synapse. Here we will give a couple of examples of the complexity of these opposing effects.

Opposing pre-and post-synaptic effects of DA on the LP-PD synapse

The pacemaker kernel of the pyloric network is an electrically coupled trio of the Anterior Burster (AB) and two Pyloric Dilator (PD) neurons (Fig. 2). These neurons oscillate endogenously in the presence of the appropriate neuromodulators, and they inhibit all the other neurons in the network. These follower cells resume bursting by post-inhibitory rebound at different rates. The only neuron providing any feedback to the pacemaker kernel is the Lateral Pyloric (LP) neuron, which uses glutamate to inhibit the two PD neurons, thus (through electrical coupling) also inhibiting the AB burster neuron. We, along with Jack Peck decided to look at how DA modulates graded synaptic transmission at this synapse. Dopamine very markedly strengthens this LP→PD synapse, as can be seen in Fig. 3.

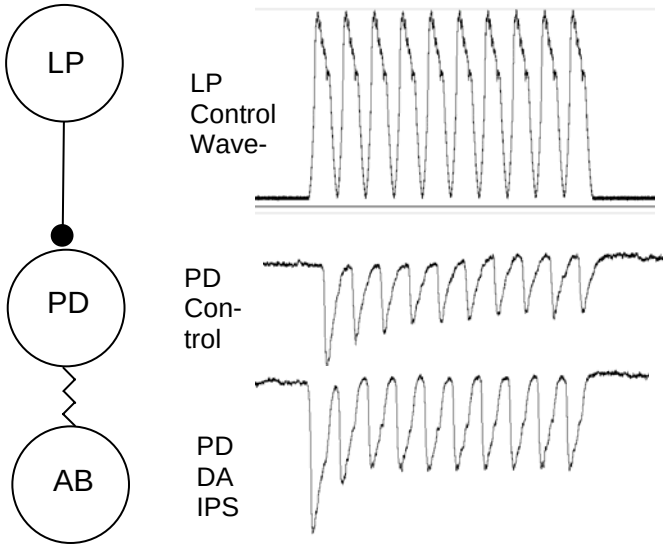

Fig. 3: Dopamine enhances the LP→PD synapse. Top: LP voltage-clamped and driven with an average smoothed oscillation. Middle: Post-synaptic PD response. C: Enhanced response in the presence of DA.

Here, we isolated the synapse, and drove the LP cell in voltage clamp with a series of realistic waveforms that are the smoothed averages of the normal LP oscillation. This evokes a graded IPSP in the PD neuron, which depresses slightly to a steady state level that would be seen during a normal pyloric rhythm. DA dramatically strengthens this synapse, increasing both the initial IPSP amplitude and the steady state IPSP at the end of the series. Indeed, DA strengthens all LP synapses in the STG.

A synapse can be strengthened either pre-synaptically, by releasing more transmitter, and/or post-synaptically, by responding more strongly to the released transmitter. We can look at these independently in this simple system. Many (though not all) of the pre-synaptic mechanisms to strengthen a synapse funnel into increases in calcium entry into the terminal, which serves as the final trigger for transmitter release. Accordingly, we looked for DA modulation of calcium entry into LP terminals using calcium imaging with multiphoton microscopy. The LP terminals can be distinguished as varicosities in the neuropil, which were shown by David King to be filled with synaptic vesicles; voltage-dependent calcium entry is concentrated at these varicosities. Using Calcium Green as an indicator, Peter Kloppenburg and Warren Zipfel[4] showed that at most LP varicosities, DA evoked a significant increase in voltage-dependent calcium accumulation (Fig. 4).

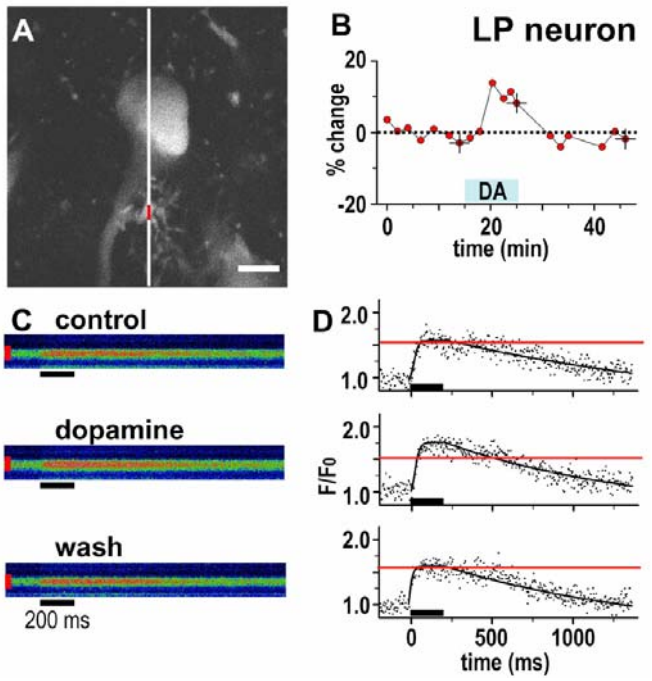

Fig. 4: Dopamine enhances voltage-dependent calcium accumulation in LP pre-synaptic terminals. A: LP neuron filled with Calcium Green-1. B. Time course of change in calcium signal during DA application. C. Samples of calcium signal change during 100 msec voltage step from -50 to 0 mV. D. Analysis of the signal showing the enhanced calcium response during DA.

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trated at these varicosities. Using Calcium Green as an indicator, Peter Kloppenburg and Warren Zipfel[4] showed that at most LP varicosities, DA evoked a significant increase in voltage-dependent calcium accumulation (Fig. 4). This effect reversed after removal of DA, just as the strengthened synapses reverted to their normal amplitude after DA washout. We confirmed this imaging result using voltage clamp measurements of calcium currents from the LP neuron: DA enhances $I_{Ca(V)}$ in the LP neuron[5]. These results suggest that at least part of DA's enhancement of the LP synapse is presynaptic.

To study the post-synaptic effects of DA on the PD neuron, we simplified the situation by isolating the PD from all synaptic input by photoinactivating the LP neuron. Then we replaced the LP synapse with iontophoretic application of its transmitter, glutamate. Here we had a real surprise, as seen in Fig. 5: even though DA strongly enhances the LP→PD synapse, it dramatically reduces the PD response to LP's transmitter, glutamate[6]. This effect appears to be a combination of reduction in the synaptic response and a general reduction in the input resistance of the PD neuron, which reduces its responsiveness to all synaptic inputs.

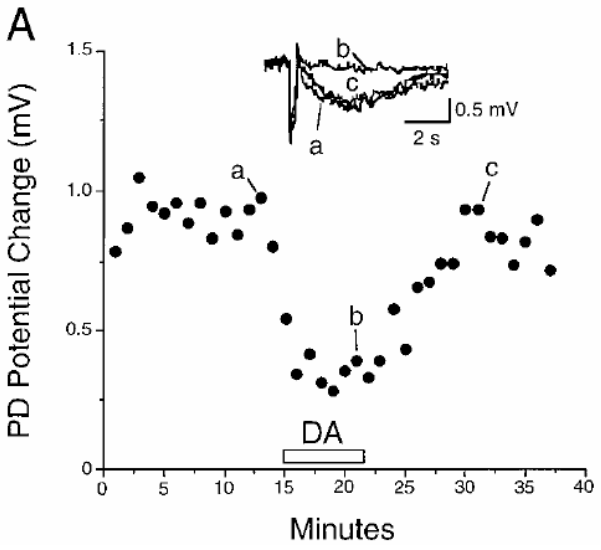

Fig. 5: DA reduces the post-synaptic PD response to glutamate iontophoresis. Glutamate is the LP transmitter.

This is a typical example of opposing effects of DA on a synapse. DA enhances the strength of the synapse, and enhances pre-synaptic calcium currents and voltage-activated calcium entry into LP terminals, but at the same time it dramatically reduces the PD post-synaptic response to LP's transmitter. Without the reduction in PD responsiveness, this synapse might become strong enough to disrupt the motor pattern. Thus, these opposing actions could reliably stabilize the extent to which DA strengthens this synapse.

Opposing effects of Dopamine on graded and spike-evoked transmission at the LP→PD synapse

There is another novel opposition at this synapse. As we said above, the pyloric neurons release transmitter by both spike-evoked release and graded release. Amir Ayali looked at the effects of DA modulation on these two forms of transmission at the output synapses of the LP neuron[7]. He found that DA enhances graded transmission at the LP→PD synapse, as described above, but surprisingly, DA reduces spike-evoked transmission at the same time (Fig. 6).

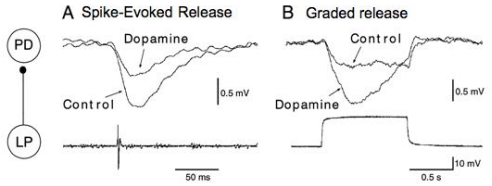

Fig. 6: DA decreases the size of the spike-evoked IPSP at the LP→PD synapse (Left) while enhancing the size of the graded IPSP at the same synapse (right).

This reduction in spike-evoked transmission correlates linearly with DA reduction in input resistance in the post-synaptic PD neuron, a post-synaptic mechanism of action. A similar result was observed at the LP →VD synapse. These surprising results suggest that there are some basic differences between spike-evoked and graded transmitter release at the pyloric synapses. One possibility is that they are mediated by different calcium channels, as has been found in the leech (Jin Lu et al., 1997), and DA modulates one class but not the other. This mechanism also stabilizes the LP inhibition of the PD neuron by strengthening graded transmission while simultaneously weakening spike-evoked transmission.

Multiple actions of dopamine at PY terminals of the PY→LP synapse

A third example is seen at the synapses of the pyloric constrictor (PY) neurons. There are 8 of these cells, with somewhat different properties: a majority of them are excited by DA. However, all the PY output synapses are significantly strengthened by DA. Indeed, at PY→LP synapses, in the absence of neuromodulators, the chemical component of the synapse often falls silent. Addition of DA reactivates the synapse so that PY excitation generates a significant IPSP in the LP neuron[8] (Fig. 7).

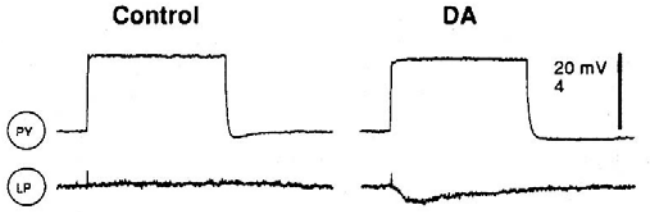

Fig. 7: Dopamine activates a silent PY→LP synapse.

Again, this synaptic enhancement can occur by pre-and/or post-synaptic mechanisms. Post-synaptically, the isolated LP neuron shows an enhanced response to iontophoresis of the PY transmitter,glutamate, consistent with the strengthened synapse[9]. Pre-synaptically, however, our calcium imaging studies of voltage-dependent calcium entry into PY varicosities uncovered an unexpected complexity in DA responsiveness[10]. About 40% of pre-synaptic varicosities responded to DA with an enhanced calcium entry, consistent with the strengthened synapse. Another 40 % showed no change at all. However 20% of the varicosities responded with an unexpected and significant reduction in voltage-dependent calcium entry during DA application (Fig. 8).

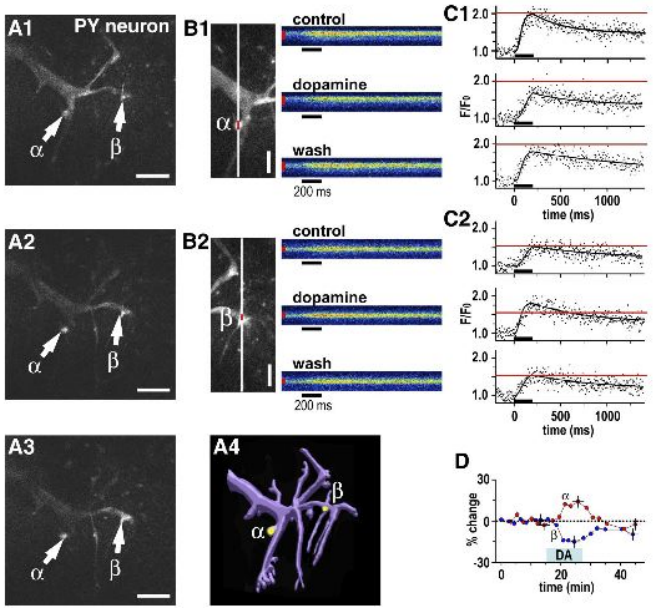

Fig. 8: Dopamine has opposing effects on different PY presynaptic terminals in the same neuron. A: Figure showing the locations of two varicosities in a PY neuron. B: Dopamine reduces the voltage-dependent calcium accumulation in the α synaptc terminal but increases it in the β terminal. C, D: quantification of the effect.

As mentioned above, the 8 PY neurons are somewhat heterogeneous, and we initially proposed that these varying responses of PY varicosities to DA arose from the different PY neuron subtypes. However, this turned out to be wrong. In 17 experiments we simultaneously imaged calcium accumulation in two varicosities in a single PY neuron; we found all combinations of increases and decreases in calcium accumulation in the two sites. Significantly, in six neurons, the calcium response increased with DA at one varicosity but decreased in the other varicosity, two opposing effects on varicosities of the same neuron (Fig. 9).

The situation for the PY synapses is thus a different example of opposing effects of DA to regulate synaptic strength. All the PY output synapses are enhanced by DA. However, only a subset of the PY varicosities showed increased voltage – dependent calcium accumulation during DA application, while a significant number showed the opposite, a decrease in calcium accumulation. On average, the net response is an increase in calcium entry, and we confirmed this in voltage clamp measurements from the soma, which would give us a net effect of all the calcium responses[5]. We interpret these data to suggest that DA is once again regulating the strength of the PY output synapses, this time not by having opposing pre- and post-synaptic effects, but by having opposing pre-synaptic effects in different PY terminals. In *P. interruptus*, each PY neuron makes multiple physical synaptic contacts onto each of its post-synaptic target neurons (P. Kloppenburg, unpublished). If some of these terminals release more transmitter while others release less during DA application, the net effect will be to limit the maximal increase in synaptic strength. Again, this may function to limit the degree of modulation of these synapses to retain the network in a functional state.

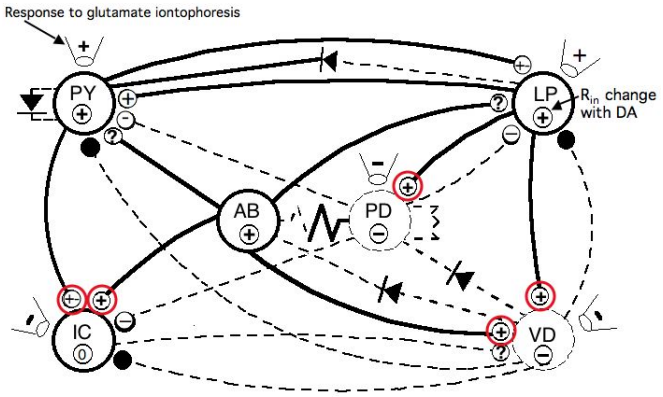

Fig. 9: Summary of effects of dopamine on all the pyloric synapses. Synapses strengthened by DA are shown with heavy lines while those weakened by DA are shown with dotted lines. Symbols within the neurons show effects of DA on the input resistance of the neuron. Symbols within pipette tips show DA effects on the response to glutamate, the transmitter of the PY, LP, IC and AB neurons. Symbols within the nerve terminals show effects of DA on voltage-sensitive calcium accumulation in the terminals. Terminals with questions marks have not yet been measured.

Such opposing changes in DA modulation of synaptic strength are not rare. As seen in Fig. 9, the circled synapses are those where we have detected opposing effects of DA. So many cases argue that they are not simply "mistakes", but rather that they serve a real purpose to constrain the changes in synaptic strength such that the network continues to function appropriately in the DA-modified state.

Conclusion

Opposing effects of DA in the pyloric network are not limited to synapses. If there were space, we could also write an equally long report about the opposing effects of DA on the ionic currents that shape the intrinsic firing properties of the neurons. Once again, it appears that DA activates some cur-

rents that would work against its overall effect on the cell's firing properties, suggesting that these currents help to constrain the degree of modulation of the cell, maintaining its activity within a range that is functional for the network.

While these detailed studies of the pyloric network provide perhaps the clearest examples of the pluses and minuses of modulator action on networks, there are hints that it occurs elsewhere as well. For example, Brian Burrell and Qin Li[11] found that when LTP is induced in a leech central synapse, LTD is always also induced, and the resulting synaptic change reflects the sum of these opposing processes. Goldfarb et al.[12] showed that serotonin, acting on different receptors, simultaneously enhances and inhibits glutamate's ability to evoke release of norepinephrine in the hypothalamus. In the basolateral amygdala, Power and Sah[13] showed that acetylcholine, acting on metabotropic muscarinic receptors, simultaneously enhances the apamin-sensitive SK-type $I_{K(Ca)}$ while blocking the apamin-insensitive slow $I_{K(Ca)}$: The inhibitory effect predominates during bath application of ACh, while the excitatory effect predominates during focal application onto the soma and proximal dendrites.

These results show that it is important to look at both the pluses and the minuses of modulatory actions in a system. We do not know how general this phenomenon is, and would love to hear of your examples of opposing actions of modulators in your system.

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Neuroethological studies in freely-behaving echolocating bats: past, present, and future

Nachum Ulanovsky (nachum.ulanovsky@weizmann.ac.il)

Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel.

http://www.weizmann.ac.il/neurobiology/labs/ulanovsky/

A few months ago, after telling a stranger that I am studying bats, he exclaimed: "Bats! These creatures must be the pinnacle of evolution!". It remains debatable whether indeed bats are the pinnacle of evolution, or perhaps we are – or none of the above – but certainly bats have captivated the imagination of people, scientists and non-scientists alike. Mammals that can fly; can navigate and avoid obstacles in complete darkness; can live almost ten time longer than rats or mice – the biology of bats is a fascinating topic. Neuroethologists have also been fascinated by these animals, and studied extensively the neural basis of their extraordinary behavioral capabilities; this endeavor resulted in some of the greatest achievements of neuroethology, as can be witnessed by opening any neuroethology textbook.

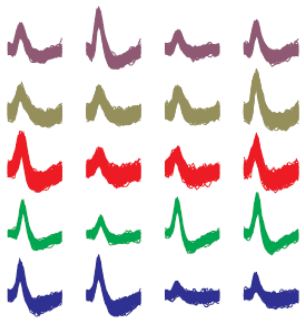
One could argue that the "holy grail" of neuroethology is to elucidate the neural basis of behavior in freely-behaving animals.

Fig.1. Bat species used as a model animal in my lab: the Egyptian fruit bat, Rousettus aegyptiacus. Photo courtesy of M. Brock Fenton.

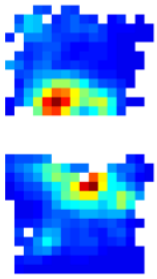
However, in bats, as in many other model animals of neuroethology, much of the research was done not in freely-behaving animals, but rather in animals that were restricted not to move. The stimuli used were also oftentimes not entirely natural: for example, when studying the neural basis of the bat sonar system, most studies (with a few notable exceptions) utilized artificially produced pulse-echo pairs, rather then letting the bat vocalize and recording the response to the actual returning echo. This situation – of studying the neural basis of behavior in non-behaving animals – has two underlying reasons, each of them a very good one: First, the technical difficulty of performing electrophysiological recordings of single neurons in freely behaving animals (this still remains much of a problem when studying invertebrates, for example). Second, the difficulty of controlling the behavior in a freely-behaving animal. Certainly using a restrained animal allows overcoming both of these difficulties. Nevertheless, the second issue can be overcome by training the animal to perform a carefully designed and well-controlled behavioral task, as has been done in monkeys and in rats for decades. In this article, I would like to argue that, at least in the case of bats, the first problem can also be overcome: we are now at a stage when the technical difficulty of recording in freely behaving bats (and indeed in many other vertebrates) does not constitute a fundamental problem anymore.

Having earned a B.Sc. in Physics, and a Ph.D in neural computation – doing electrophysiological recordings in cat auditory cortex (Ulanovsky et al., 2003) – I, too, was fascinated by the biology and physics of bats. My first studies in bats were field studies, where we demonstrated for the first time the existence of a jamming avoidance response (JAR) in two closely-related bat species in Israel and in the US: these studies have shown that, similar to JAR in *Eigenmannia* and some other species of weakly electric fish, bats shifted their sonar call frequency to avoid overlap with the frequency of conspecific calls (Ulanovsky et al., 2004; Gillam, Ulanovsky, McCracken., 2007). My true passion, however, was in actually conducting recordings of neural activity in freely-behaving bats, in order to understand the neural basis of behavior – more specifically, the neural basis of learning and memory in one of the brain's most fascinating areas, the hippocampus. The hippocampus is crucial for episodic and spatial memory in animals and humans, and bats constitute a wonderful animal model for hippocampal studies, since they possess an outstanding spatial memory, covering many spatial scales: from > 1000-km annual migrations in some bat species, down to 3-D spatial memory on a 1-cm scale in lab conditions (Ulanovsky and Moss, 2008). To achieve this goal, I went to do a postdoc at Cindy Moss's BatLab at the University of Maryland, where I took head-on the technical difficulties of recording neural activity in a tiny animal like the big brown bat (*Eptesicus fuscus*), which weighs 15 gr: to this end, I adapted tetrode-recording techniques to studies of neural activity in the hippocampus of crawling bats (as to flying bats, see below). Tetrodes are bundles of four wires with four recording points at the end: when putting four tetrodes (sixteen recording channels altogether) into a 2.1-gr microdrive, they allow high-fidelity recordings of single-neuron activity from several simultaneously-active neurons. Tetrodes allow recording spiking activity from freely behaving animals with quality and stability that regular electrodes do not allow (the basic principle of spike-sorting of tetrode data relies on using the relative amplitudes of the spikes recorded on the four channels of each tetrode, as illustrated in Fig. 2). These recordings showed that the bat hippocampus contains "place cells" similar to rodent hippocampus: these are neurons that become active when the animal passes through a restricted region of the environment, termed the "place field", and are thought to be crucial for spatial memory and navigation. The place cells that we found in the bat hippocampus (e.g. Fig. 1) were as common, as spatially-selective and as stable as the place fields in rat hippocampus. Some other aspects of the neural activity in bat hippocampus, such as the theta oscillation, turned out to be surprisingly different than in rodents – for details see our recent article that described these first recordings of neural activity from the bat hippocampus (Ulanovsky and Moss, 2007). I now wish to turn to briefly describing some future plans for neurobiological studies in freely behaving bats.

Plans for my lab include purely behavioral studies of bat echolocation, as well as of bat spatial memory. In addition, neurophysiological studies will be pursued in freely-crawling bats, both on mazes and on traditional Y-type platforms – these studies are technically very similar to the recordings described above. But the most exciting new research direction involves recording single-unit activity from freely *flying* bats. To achieve this goal, my students and I are making two changes. First, we are starting to use a lightweight neural telemetry system that allows recording wideband (spike) data without the use of wires. Figure 3 shows example of spikes recorded from the big brown bat hippocampus using this telemetry system (the four traces were recorded from the four channels of one tetrode). Second, we switched to using a much larger bat species, the echolocating fruit bat *Rousettus aegyptiacus* (see photo), which is easily able to carry our miniaturized telemetry system that weighs a total of 9 gr (including batteries).



Spike waveforms of five pyramidal neurons recorded simultaneously in bat hippocampal area CA1



Place fields of bat hippocampal place cells

Fig. 2 Neural recordings from bat hippocampus. Left: spike waveforms of five simultaneously-recorded neurons from bat hippocampal area CA1, recorded using a tetrode. Rows show the five neurons, columns show the four channels of the tetrode: one can clearly see the different spike amplitudes on the different tetrode channels, which forms the basis of the spike-sorting technique for tetrode data. Shown are all the spike waveforms recorded during one day on this tetrode, superimposed (several thousand waveforms in total). Right: Place fields of two place cells, red color = maximum activity of the neuron. From Ulanovsky and Moss (2007).

These three technological advances – (i) tetrode recordings, (ii) neural radio-telemetry, (iii) using a large bat species – will allow us to address a series of fascinating questions. For example, are there 3-D place cells in bat hippocampus – and more generally, what is the nature of 3-D spatial representation in the mammalian brain?

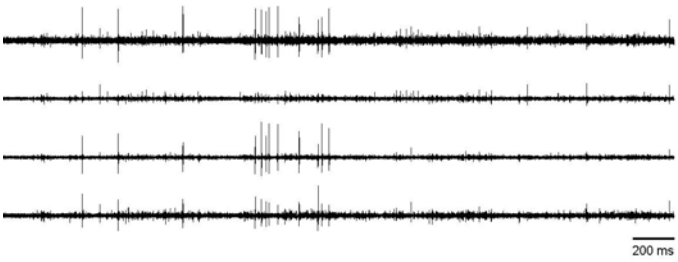


Fig. 3 High-quality spike recordings from bat hippocampus using a specialized neural-telemetry system.

Some attempts have been made to answer the question of 3-D spatial representation in rodent hippocampus, in experiments that were done either on earth or on a NASA space shuttle (Knierim et al., 2000; Knierim and McNaughton, 2001), but answers remained elusive; instead, recording from a freely flying mammal, the bat, will provide a much more natural way to address this issue. Another interesting question is related to the bat's natural transition between behavioral echolocation modes: when foraging for food or during navigation, the bats use a low rate of echolocation calls ('search phase', or navigation mode), but when the animal starts to approach a target or an object it wishes to land on, the bat increases the rate of its echolocation calls in a characteristic manner ('approach phase'). This behavioral transition is easy to detect using a microphone, and it would be of great interest to examine how neural activity in the hippocampus – a navigation related area – is modulated by transitions between a navigation mode and a non-navigation mode. I believe that these and other neurophysiological studies in freely behaving bats will broaden our understanding of behavioral neurobiology across species.

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In Memory of Dietrich Schneider

30th July 1919 – 10th June 2008:

Karl-Ernst Kaissling and R.A. Steinbrecht
Max-Planck-Institut für Ornithologie
82346 Seewiesen, GERMANY

(translated with permission by Ann Thorsen from *Mitteilungen der Deutschen Zoologischen Gesellschaft 2008*)

On the 10th of June, 2008, Professor Dr. Dietrich Schneider died after a brief period of severe suffering. One of the pioneers of modern olfactory research, he was the first to use electrophysiology to investigate the sense of smell, by directly recording the responses of single sensory neurons to the odour stimulus. His success depended crucially on his choice of the silk moth as experimental animal, because its males are very sensitive to the sexual attractant released by the females — as by now not only experts in the field but also every educated layman knows. This proved to be a model system for olfaction that offered many advantages. The adequate stimulus, the pheromone bombykol, is a relatively simple molecule with

obvious biological relevance, and the receiving organ, the male antenna, is optimized to capture even the slightest amounts of odorant. Furthermore, each of the many thousand sensory hairs, which are arranged on the antenna to form an odorant sieve, is readily accessible to the physiologist's electrodes. For the first time a quantitative analysis of the olfactory sense became possible, and the school that Schneider established in Munich, at the Zoological Institute, and then expanded at the Max-Planck-Institute for Behavioural Physiology in Seewiesen, was soon pointing the way towards research that would be carried out by students of olfaction worldwide.

Dietrich Schneider was born in 1919 in Berlin. Having qualified for university admission in 1937, he first studied biology at a teachers' college in Frankfurt on Oder and then in 1938 moved to the University of Berlin, but as early as 1940 he was drafted into military service. In North Africa, in 1943, he began four years as a prisoner of war, during which period he was transferred from Algeria to the USA and England. While a prisoner he was nevertheless able to spend some time continuing his studies, so that in 1949, only two years after returning home, he obtained a PhD in Göttingen with specialties in zoology, botany and physiology. His thesis research, on the electrophysiology of saltatory nerve conduction, was carried out in the laboratory of Hansjochem Autrum. In the same year he married Heidwig Intemann, with whom he had three children. Soon thereafter he was appointed scientific assistant to Alfred Kühn at the MPI for Biology in Tübingen; among the things he investigated here were the field of view of frogs and their escape and predation behaviour, and finally the light-oriented growth of marine Bryozoa.

At this time Peter Karlson and Adolf Butenandt were also working in Tübingen, on the isolation of bombykol, the first chemically characterized insect pheromone. Schneider's interest thus aroused, he began to make electrophysiological measurements of the silk-moth antenna. He recorded the summated responses of the olfactory cells, the electroantennogram, which enabled him to make the first quantitative analysis of the olfactory sense. Soon he began to record the responses of individual, identified olfactory cells. It should not go unmentioned here that the faculty of the University of Tübingen failed to recognize the broad significance of these discoveries and hence did not accept them as grounds for an academic career (hablitation) there. Therefore in 1958 Schneider transferred to the Zoological Institute of the Ludwig-Maximilians-Universität in Munich, where he obtained a professorship in 1959 with his study on the growth and phototropism of the Bryozoa.

In 1962 the Department of Comparative Neurophysiology was established for Dietrich Schneider at the MPI for Psychiatry. In 1964 he became a scientific member of the MPG and was appointed Director of the MPI for Behavioural Physiology in Seewiesen. Then in 1965 he was given the title Honorary Professor at the Ludwig-Maximilians-Universität in Munich. Foremost among his research subjects were insects' peripheral identification and discrimination of odour substances and mixtures thereof, as well as the physiology and structure of the olfactory organs. However, his multifaceted approaches to research and the broad spectrum of methods employed also led to work on the production by insects of their own odorants, the structure of the odorant-producing glands, the enzymatic decomposition of odorants in the olfactory organ, the phylogenetic relations between insect species with respect to their pheromones and how they are identified, which nerve centres are used to process the olfactory signals, and the odour-controlled orientation behaviour of insects. Later Schneider again turned to an area, which at that time was largely ignored, the relationships between insects and plants, and became one of the pioneers of chemical ecology. He devoted himself to this fascinating subject with special intensity even after acquiring emeritus status in 1985.

Dietrich Schneider was always a critical and committed partner in discussions of questions related to the politics of science. He spent an especially large amount of time and energy on setting up the International Center for Insect Physiology and Ecology (ICIPE) in Nairobi, Kenya, and was one of the international members of its Governing Board for many years. Until the end, he observed the development of the Max Planck Society with great interest. Although he was rather sceptical about the planned establishment of new Max Planck Institutes in distant foreign countries, he was very much in favour of international collaboration. This is evidenced not only by his many, often several-month research visits abroad, to Sweden, Yugoslavia, many places in the USA, and in Kenya, but also

by the impressive number of scientists from all over the world who undertook research as visitors to his institute in Seewiesen, with more than a few of whom he developed close friendships.

Schneider's achievements were soon recognised, and he was offered positions abroad, e.g. in Utrecht or Los Angeles, but these were declined. Throughout his long research career he was honoured in many ways. For instance, beginning in 1962 he was among the organisers of the first International Symposia on Olfaction and Taste; he was a member, e.g., of the American Academy of Arts and Science in Boston (from 1971), the Leopoldina (from 1975), which later awarded him the Cothenius Medaille, and the Bavarian Academy of Sciences (from 1977). He was chosen to be the John Prather Lecturer at Harvard University in Boston, became the First Distinguished Visiting Professor of the Center for Insect Science at the University of Arizona, Tucson, and in 1991 was awarded the Silver Medal of the International Society for Chemical Ecology. In 1992 he became an Honorary Doctor at the University of Regensburg.

He himself, however, never regarded these many awards as very important; grandiloquence and pathos were not his style, and with his mischievous Berlin humour he reduced quite a few big shots — and he encountered many of those — to human proportions. This humour also defused tense situations and created the relaxed professional environment that everyone who had the privilege of living and working under his roof still remembers so fondly today. At the same time he was relentless towards himself in his personal commitment to research, and the same was required of his colleagues. He was not a strict supervisor, believing that incentive must come from within; this was ensured by his own passion and boundless curiosity, combined with his joy and enthusiasm for communicating new findings, opening them to critical discussion and exploring their implications. Thus we, his students and coworkers, enjoyed a degree of freedom in the choice of our research goals, approaches and methods that is hardly imaginable today; all that counted was the result. We are also grateful to him for sending us early onto the international stage, and thus ensuring that we met the major contributors to our field.

A very special experience was going on "safari" with Dietrich Schneider. Prof. Franz Huber, to whom he was bound by a friendship lasting over 50 years, writes "whoever has seen Dietz hunting his butterflies with hat and net, or seen him sitting at the table in his hotel room at 3 a.m. while preparing the pheromone-loaded hair pencils of a moth, will get a slight impression of the commitment of this man, who was driven by curiosity and to whom finding something new meant everything." His wife Heidwig also became "hooked" on Africa, and it was she who while there made the crucial observation that *Danaus* moths acquire the alkaloid precursors of one of their sexual pheromones from wilting heliotrope plants.

Much more could be reported here, because Dietrich Schneider was a sociable man and lively storyteller, and brought his rich research career to life for us with his consistently humorous tales. For — in the words of Gabriel Garcia Márquez — *"life is not what we have lived, but what we can remember, and how we remember ourselves, in order to tell about it."* Our sadness over the death of Dietrich Schneider, which we share with all his family members and friends, is alleviated by the happy knowledge that we were allowed to spend so many years together with him.

Brief Report on the Executive Committee meeting of the ISN

Boston, July 19, 2008

Participants:

Fred Delcomyn (Treasurer)
Albert Feng (Past President)
Alberto Ferrus (Organizer of the 2010 ICN)
Katalin Gothard (Secretary)
Linda Hardwick (Business Manager)
Martin Heisenberg (President)
Paul Katz (President-Elect)
Ed Kravitz (Past President)

Agenda:

Opening Remarks (Martin Heisenberg)
Financial Resport (Fred Delcomyn)
Business Report (Linda Hardwick)
Preparations for the ICN in Salamanca (Alberto Ferrus)
Congress Committees
Membership Development (Linda Hardwick)
Strategic Planning Committee (Paul Katz)
Heiligenberg Student Travel Award Committee (Paul Katz)
Timing of IBN and GRC (Martin Heisenberg)
Outreach Program for Emerging Countries I (Albert Feng)
Outreach Program for Emerging Countries II (Martin Heisenberg)
Website (Martin Heisenberg)
Educational Material on the Web (Martin Heisenberg)
Textbook (Martin Heisenberg)
Dues (Martin Heisenberg)

Summary of discussions:

1. The Society is in good financial standing. This is due to the judicious investment decisions of the past and current treasurers.
2. The financial policy of the Society needs to be changed to afford more flexibility for organizing Congresses in foreign countries.
3. The pattern of increasing/decreasing membership during the congress year and off-congress years continues. The Society needs to do a better job recruiting new members to bring

new blood into it and retaining existing membership to remain vibrant. The current membership benefits are:

- Registration discount for Congresses
- Triennial Congresses
- Young investigator fellowships and student travel awards
- Scholarly "home" for neuroethologists
- Discount for the two affiliated Journals (*J. Exp. Biol*. and *J. Comp. Physiol*. *A*)
- Newsletter
- Web site, listserv

4. The EC discussed proposals for additional benefits that will be submitted for approval to the ISN Council. These include:

- Short-term travel awards for students and postdocs who would like to travel to a lab to learn a new technique or establish collaborations.
- Congress attendance award for students, postdocs and young faculty from developing countries.
- Create Fellows of the Society. This would be a prestigious, honorary position bestowed on members.
- Re-design the website and transform it into a useful resource for the members.
- Increase the visibility of the ISN by lobbying in the interest of the society and its members

5. In preparation for the 2010 International Congress of Neuroethology in Salamanca the following decisions have been made:

- Dates: August 4-7, 2010
- The local Organizing committee will be chaired by Alberto Ferrus, who will be assisted by Miguel Merchan, Professor of Anatomy, who works on the auditory system, and by Manolo Malmierca.
- The Congress will be held in a modern and spacious conference center in the beautiful historic city of Salamanca in central Spain. Salamanca is a short distance away from Madrid (219 km) and easily reachable via hourly buses and trains.
- The Program Committee will be constituted shortly following consultation of the Council.
- The Local Organizing Committee and the Program committee will benefit from a retroactive survey of the Vancouver Congress - this is coming to you soon.

6. The Society will increase its outreach activities in the developing countries by "exporting" advanced courses and by assisting local neuroethologists to attend our Congress and establish international collaborations.

7. Next EC meeting will be in late May 2009 in Würzbug.

The recipients of the 2008 Heiligenberg Awards

Congratulations to the recipients of the 2008 Heiligenberg Awards! This year the ISN will contribute $700 toward travel and congress-attendance expenses of the following recipients.

1. Andrew A. George (USA) will attend the Gordon Research Conference for Neuroethology, UK
2. Victoria S. Arch (USA) will attend the 6th World Congress of Herpetology, Brazil.
3, Geremy Corfield (New Zealand) will attend the Acoustic Communication by Animals, Oregon.
3. Laura Hausmann (Germany) will attend Gordon Research Conference for Neuroethology, UK
4 Olle E. Lind (Sweden) will attend the Gordon Research Conference for Neuroethology, UK
5. Faviana Luca Alves (Brazil) will attend the Gordon Research Conference for Neuroethology, UK
6. Damian Oliva (Argentina) will attend the International Conference on Invertebrate Vision
7. Srdjan Maksimovic (USA) will attend the International Conference on Invertebrate Vision

Positions available

Behavioral Studies of Molecular and Biophysical Basis of Light-dependent Magnetic Compass in Larval Drosophila

A **postdoctoral position** is available in the lab of Dr. John Phillips at Virginia Tech to study light-dependent magnetoreception in larval Drosophila. This project is part of an ongoing effort to characterize the molecular and biophysical basis of the light-dependent magnetic compass using recently developed behavioral assays of magnetic compass organisms in larval Drosophila (Dommer et al. 2008. J. Insect Physiol. 54: 719-726, and C57BL/6 mice (Muheim et al. 2006. Learn. Behav. 34: 366-373). Research will involve behavioral studies of exposure to different lighting conditions and to low level radio frequency fields, as well as testing of mutant strains targeting candidate molecules (e.g., cryptochromes). Experience working on animal spatial cognition, insect behavior, photoreception, or Drosophila behavioral genetics preferred. Position includes a competitive salary and fringe benefits. Funding is available for 2+ years.

Interested candidates should submit a curriculum vitae and statement of interest upon applying online at: www.jobs.vt.edu (Posting #080581). Three letters of recommendation should be sent via email to Dr. John Phillips at jphillips@vt.edu. Review of applications will begin July 5, 2008. If you have any questions regarding this position, please contact Dr. John Phillips at jphillips@vt.edu or 540/231-1484

Phillips lab website:
http://www.biology.vt.edu/faculty/phillips/

Virginia Tech is an Equal Opportunity/Affirmative Action Institution.

An immediate opening is available for a **Research Assistant** to join the research group in Dr. Paul Garrity's laboratory at the National Center for Behavioral Genomics (http://www.bio.brandeis.edu/genomics/) in the Department of Biology at Brandeis University. The group's focus is on characterizing the molecular basis of behavior, in particular the molecular mechanisms through which animals sense and respond to environmental stimuli such as temperature.

Primary responsibilities include assisting with molecular and genetic experiments using Drosophila. Specific duties include histopathology, Drosophila behavioral assays, PCR and molecular cloning, as well as ordering and maintaining laboratory supplies and Drosophila stocks. Good organizational skills, motivation and an ability to work independently are all important.

Requirements: A B.S./B.A. in biological sciences (or an M.S. in biological sciences) and experience in genetics and/or molecular/cellular biology. Previous experience with Drosophila and/or molecular biology helpful.

In addition to a CV, the names, e-mail addresses and telephone numbers of three references should be submitted to jdkaplan@brandeis.edu and pgarrity@brandeis.edu

Add our Link to Your Website!

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