The Golden Age of Comparative Neuroethology on Display in Japan

Paul S. Katz

Neuroscience Institute, Georgia State University, Atlanta, Ga., USA

I recently returned from an incredible trip to Sapporo, Japan, where I attended the eleventh International Congress of Neuroethology (ICN) (<http://www.icn2014.jp/>). The very first ICN was also held in Japan in 1986. There were 304 participants at that first congress (142 from overseas and 162 from Japan). Twenty-eight years later, there were 630 participants with 416 coming from 21 countries outside of Japan. This was my first visit to Japan and I learned firsthand about the culture of elegance, grace, and perfection. This applied to the conference itself, which was incredibly well managed.

Neuroethology is of course the study of the neural basis of natural behavior. Researchers in the field often point to Krogh's principle as a justification for studying the neural basis of behavior in 'non-model' organisms, namely that an organism should be chosen because it is the easiest with which to study a particular problem [Krogh, 1929]. Thus, barn owls were chosen for studying sound localization because of their champion abilities at catching prey with passive hearing [Konishi, 2003]. Similarly, the jamming avoidance response was studied in the electric fish because it offered an opportunity to explore sensorimotor integration of an entire behavior [Heiligenberg, 1980]. The field of neuroethology became synonymous with these specialized animals, their abilities, and the pioneering researchers who studied them.

One of those early pioneers of neuroethology, Masakazu (Mark) Konishi, was honored at this conference with a symposium in his name. There were four speakers who each had worked with Mark at some point in their careers and whose works were shaped by Mark's insight. Mark is best known for his work on sound localization in barn owls and for his work on birdsong learning. Mark was also honored with the awarding of the first Konishi Neuroethology Research Awards to four young investigators. It was wonderful that Mark was able to attend this conference and particularly that he was accompanied by Walter Heiligenberg's son. Walter was an early pioneer of work on the jamming avoidance response in electric fish.

Other icons in neuroethology were honored at this conference by being named Fellows of the International Society for Neuroethology. The Fellows inducted this year were Franz Huber, Eve Marder, Ed Kravitz, Tom Collett, Darcy Kelley, and Tom Cronin. They were chosen for their research, their leadership in education and outreach, and their extraordinary service to the field of neuroethology.

Now, decades after the first ICN, we see that there is still active research on classic neuroethological organisms, which, in addition to owls and electric fish, includes bats, honeybees, crickets, and lampreys. However, there is a far greater diversity of organisms than ever before, including:

jellyfish and rice fish, cuttlefish and cavefish, jumping spiders and spider monkeys, praying mantis and mantis shrimp, and even laboratory mice and rats, to name just a few that were represented in the presentations.

At the time of the first ICN, the fruit fly, *Drosophila melanogaster*, and the nematode, *Caenorhabditis elegans*, were primarily genetic model organisms; there was little hope in 1986 of recording and stimulating neurons to study the neural basis of behavior in these tiny creatures. However, that has clearly changed with modern optogenetic and recording techniques. At this meeting, there were over 40 presentations on the neuroethology of *Drosophila* and *C. elegans*, including a plenary lecture on the *Drosophila* feeding circuitry by Motojiro Yoshihara from the National Institute of Information and Communications Technology, Kobe. There were also talks and posters on *Drosophila* decision-making, vision, sleep, learning, and courtship.

The point of this zoological diversity is not to collect interesting tidbits from around the animal kingdom, but to elucidate general principles. Neuroethology is now making good on that promise. Studying a single species can lead sometimes to false conclusions about general principles. For example, zebra finches have been the species of choice in studying the details of songbird circuitry. Many labs around the world use the zebra finch as a 'model' or-

ganism. However, if you look at the songs of closely related Australian finches, as Sarah M. Woolley of Columbia University explained in a plenary talk, the zebra finch is the outlier; its song is much more atonal than those of its sister species. So, when testing whether there is an auditory filter for song, you would not be able to see the full picture unless you understood the diversity of the sound signatures.

In a very challenging plenary lecture, Barbara Finlay of Cornell University drew together data from many developmental stories to create an integrated view of how the mammalian brain develops using conserved mechanisms. She has developed an evo-devo approach that precisely explains species differences in the cerebral cortex based on a common set of rules for generating neurons.

Malcolm MacIver from Northwestern University pointed out the importance of looking at evolutionary convergence for determining optimal biophysical solutions. In his plenary talk, he noted that a mechanically optimized solution for swimming with elongated fins has evolved independently eight times in both fish and invertebrates. After discussing the mathematics of this solution, he demonstrated it with a robot that was able to manage an underwater maze using an elongated ventral fin with counterpropagating waves. This design results, counterintuitively, in both increased stability and maneuverability.

Robots featured prominently in several other presentations, including a plenary talk by Ryohei Kanzaki of the University of Tokyo, who built an insect-robot hybrid mobile system that was able to navigate and find odor sources. There were even robotic flowers, built by Young Investigator Awardee Simon Sponberg of the Georgia Institute of Technology, which challenged the hovering ability of hawkmoths.

In one symposium, the comparative approach was used within a class of animals to determine the function of a brain area; the entire symposium was dedicated to the role of the central complex in insects. Fascinating talks detailed how this structure plays a role in action selection by integrating complex visual cues.

Perhaps the most audacious attempt to find commonality through a comparative approach was a session entitled 'Deep homology of circuits underlying behavioral actions'.

This was an admittedly one-sided view of the controversial proposition that struc-

tures in the insect brain are homologous to structures in the mammalian brain. In fact, one of the speakers, Frank Hirth of King's College, London, said, 'This is going to make some people upset'. The argument that he made is that a plethora of characteristics shows that the insect central complex is very similar to the mammalian basal ganglia, genetically, developmentally, anatomically, and functionally. He, therefore, suggested that it was present in a bilaterian common ancestor. However, he had no explanation for the lack of such a structure in the brains of gastropod mollusks. A highlight of that session though was the incredible work of Nicholas Strausfeld from the University of Arizona on fossil arthropods showing complexity very early in the arthropod lineage.

Although there are many examples of evolutionary convergence in nature, there are also examples of divergence. Tal Shomrat from the Hebrew University in Israel discussed neural plasticity of the octopus brain. The complex brain of the octopus evolved completely independently from that of mammals, yet its vertical lobe has characteristics clearly reminiscent of the mammalian hippocampus. Unlike other mollusks, such as *Aplysia*, the neuromodulatory actions of serotonin in this part of the octopus brain are limited to short-term effects and do not underlie long-term potentiation. Instead, long-term potentiation in the octopus vertical lobe seems to be mediated by nitric oxide and not NMDA receptors. Thus, similarities in function could be mediated by different neurochemical mechanisms across species and even in different brain regions of the same species as Shomrat also showed.

One of the highlights of this conference is hearing the talks of the Young Investigator Award recipients. The talk by Sarah Stamper of Johns Hopkins University took the jamming avoidance response of the electric fish, *Eigenmannia*, into the field. Using an array of electrodes and sophisticated signal analysis, she was able to track individual fish in their natural habitat in the Napo River in Ecuador and observe their electric organ discharges while they interacted. She had some surprising results that would not be predicted from laboratory studies.

Another highlight of the meeting for me was the Heiligenberg Lecture, which was given this year by Harold Zakon of the University of Texas. He examined the convergent evolution of electric organs in fishes.

Some of this story was also presented on a poster by Jason Gallant of the Michigan State University. They found that the same sets of genes were recruited in different lineages of fish to convert muscle cells into electrocytes. In order to serve as an electric organ, the muscle cells needed to, among other things, lose their contractile properties, grow larger, and change their expression of sodium channels. The convergence onto the same genetic solutions in different lineages suggests that evolution has a particular 'toolbox' to play with, which promotes the repeated evolution of certain phenotypes.

With the costs of sequencing rapidly declining, I expect to see a rise in such comparative transcriptomics in neuroethology. This will allow, for the first time, genetic tools to be applied to the menagerie of non-model organisms. Whereas the early neuroethologists often focused on one species, there are now more opportunities for true comparative work as tools such as genomics and transcriptomics make work on multiple species feasible. I see this as a dawning of the golden age for comparative neuroethology. The other trend is the increase in computational abilities, which will allow a greater in-depth understanding of the neural basis of behavior.

Although the ICN ran for 5 days, there were many other events before the congress. The ICN was organized in conjunction with the 36th Annual Meeting of the Japanese Society for Comparative Physiology and Biochemistry, which met the day before ICN officially started (<http://www.icn2014.jp/satellite/meeting.html>). To draw students from around the world, there were several schools and workshops, which also preceded the congress. The International Brain Research Organization held an Advanced School of Neuroethology with topics from olfactory coding to social modulation of learning behavior to evolution of birdsong complexity (<http://www.icn2014.jp/ibro/>). It ended with an intriguing workshop entitled 'Making of Humanities: Biological Roots of Mathematics and Cooperation: A joint workshop of Social Psychology and Neuroethology' (<http://www.icn2014.jp/satellite/joint.html>). The Hokkaido Neuroethology Workshops (<http://www.icn2014.jp/satellite/workshop.html>) ran for two days and covered eight different topics at a variety of levels of analysis, including: amphibian and cricket neuroethology, birdsong, bioacoustics, invertebrate learning and memory, social cognition, insect vision, and the effect of para-

sites on behavior. These workshops were very successful at increasing the overall attendance at the meeting and in providing novel venues for discussion of neuroethologically relevant issues.

The Conference was capped off with an all-you-can-eat-and-drink visit to the Sapporo beer garden. Wonderful comradery was seen while imbibing, as organizer Yo-

shitaka Oka said, 'All the beer you deserve.' The next ICN is scheduled for March 29 to April 3, 2016, in Montevideo, Uruguay. It has now been decided that the 2018 International Society for Neuroethology will take place in Brisbane, Australia. I am looking forward to these next congresses to see the progression of the comparative approach in neuroethology.

References

- Heiligenberg W (1980): The jamming avoidance response in the weakly electric fish *Eigenmannia*. A behavior controlled by distributed evaluation of electroreceptive afferences. *Naturwissenschaften* 67:499–507.
- Konishi M (2003): Coding of auditory space. *Annu Rev Neurosci* 26:31–55.
- Krogh A (1929): The progress of physiology. *Am J Physiol* 90:243–251.