



THE BUZZ



UC RIVERSIDE – DEPARTMENT OF ENTOMOLOGY
NEWSLETTER

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OLFACTORY CODING IN THE INSECT ANTENNAL LOBE

By C. Giovanni Galizia

For most insects, olfaction is the most important sense. Odors are used for mate finding, social communication, finding appropriate egg-laying substrates, or food sources. Some of these behaviors rely on highly stereotypical odors. For example, sexual pheromones emitted by female moths attract only males of their own species, amidst a variety of other odors – and even pheromones from other species – in the air. Similarly, ants follow a specific trail odor over long distances on their foraging trips. Other odors are more varied. For example, honeybees learn the odor of a flower that is rich in nectar, and communicate that odor, by means of the traces trapped in their hair, to their sister bees.

The questions that we ask in our lab are: how are odors processed in the insect's brain? And what is the molecular organization of the olfactory system?

Interestingly, the basic physiology of olfactory coding is remarkably similar across species, be it insects or vertebrates, including humans. Odors consist of volatile substances that float in the air, and hit olfactory receptors. In insects, these are on the antennae, and in some species also on other appendages, such as the maxillary palps. Each species has a characteristic

complement of a limited number of receptor cell types, defined by the olfactory receptor type that is expressed. In an adult *Drosophila*, this number is about 43, in honeybees much more. Each receptor cell responds to some, but not all, odors. Indeed, some receptor cells are exquisitely selective, and in the natural environment of a species may only respond to a single molecule, e.g., a component of a conspecific pheromone. Other receptor

their response spectrum, or the expressed olfactory receptor. All axons of the same type coalesce into a single locus, forming a spheroid structure, called the olfactory glomerulus. *Drosophila* has 43 such glomeruli, moths number about 60-70, and honeybees 160. Consequently, when an odor hits the antenna, the activity that it elicits across the olfactory receptors is transformed into a characteristic activity pattern of olfactory glomeruli.

The logic of the olfactory code resides in these patterns of active glomeruli. Because all receptors are exposed to each odor stimulus, and because each receptor type will respond to some but not all odors, and because most odor stimuli will elicit responses in more than one receptor type, the resulting code is a combinatorial one. In other words: knowing that a particular receptor type is active will not give much information about an odor, but knowing the activity pattern across all receptors of a species allows one to identify the stimulus

with confidence. The combinatorial logic greatly expands the coding capacity of the system: if each glomerulus (or receptor type) were used exclusively for a single odor, *Drosophila*, with its 43 glomeruli, would cover an olfactory space of a mere 43 odors. By exploiting its combinatorial power, it can code a much greater variety.



Cartoon view of a honeybee flying through a cloud of odors deriving from three flowers. Note the patchy and irregular distribution of odor plumes, leading to occurrences of low-concentration areas close to the source, as well as high-concentration areas far away. Also note that plumes can intermingle, creating imperfect odor mixtures, i.e. mixtures where the relative concentration of the components varies in time and space. An animal able to navigate in an olfactory environment needs to process a rapidly changing and highly complex landscape of odor plumes.

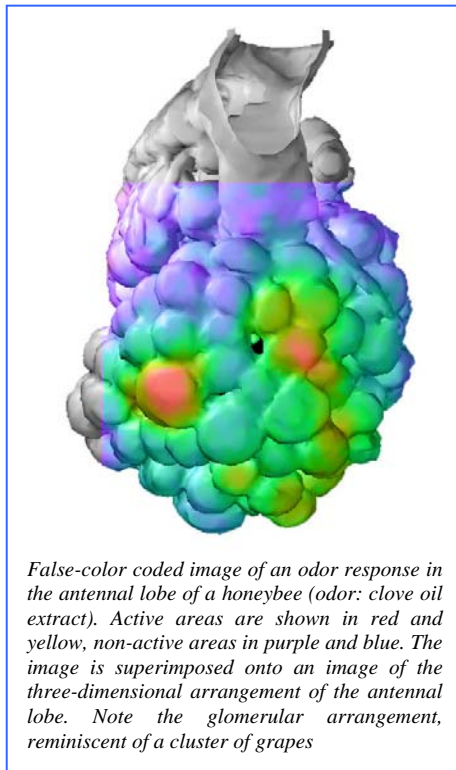
cells are more broadly tuned. A responding cell will send that information as a barrage of action potentials via its axons into the brain. Within the brain, a specialized area (i.e., the olfactory lobe, or antennal lobe) collects all that incoming information. Within this antennal lobe, incoming axons are sorted according to

It is necessary to do behavioral experiments in order to know how good an animal is at discriminating odors. In the particular case of *Drosophila*, we have no precise indication of how many odors can be encoded, but the olfactory system of the honeybee, with its 160 glomeruli, appears to be almost unlimited.

Giving importance to temporal aspects, such as spike timing, may further refine the power of these systems and several research groups, including ours, are active in this area. The role of the antennal lobe is not limited to collecting information from like receptor neurons. Rather, a dense network of local neurons interconnects those glomeruli, and further refines olfactory information. The precise role that these networks play is as yet unknown. However, their understanding is crucial for understanding how odors are encoded.

We have developed techniques to measure odor-evoked activity patterns in the antennal lobes of a variety of insects. Among these techniques, calcium imaging is the most prominent. Intracellular calcium concentration is an ideal monitor for neural activity, and there are a variety of substances that, when introduced into the cells of interest, change their optical properties as a function of intracellular calcium concentration. Some of these indicators are of synthetic origin. We have used such dyes to characterize odor-responses in moths, ants and honeybees. We found that the activity patterns are characteristic within a species. In other words, it is possible to create a physiological atlas of odor representation by naming the active glomeruli. Indeed, we could show that it is possible to 'hindcast' an odor on the basis of the elicited calcium activity pattern. Other indicators are genetically engineered. In combination with the molecular biology tools available in *Drosophila*, these can be used to dissect olfactory processing along its cellular steps. We are now characterizing the olfactory response profiles of a series of olfactory receptors in great detail. Ultimately, this endeavor will lead to knowing the complete 'olfactome' of the species, i.e., to know what the primary information is that reaches the brain. The strength of using *Drosophila* lies in the fact that the calcium indicator can be expressed specifically in all cells that express a specific receptor, and only in these cells.

Consequently, the response profile of that cell can be measured *in vivo*, with all auxiliary mechanisms in place. In a similar fashion, it is possible to selectively measure odor responses in the local neurons, or in the output cells of the antennal lobe, in order to understand the



False-color coded image of an odor response in the antennal lobe of a honeybee (odor: clove oil extract). Active areas are shown in red and yellow, non-active areas in purple and blue. The image is superimposed onto an image of the three-dimensional arrangement of the antennal lobe. Note the glomerular arrangement, reminiscent of a cluster of grapes

computations performed in the brain along the olfactory processing steps.

Using similar techniques, we have done such an analysis in honeybees. In collaboration with Christian Linster at Cornell, Ithaca, we have created a computer model of the antennal lobe, and tested what kind of connections are needed within the antennal lobe in order to explain the observed patterns. Ultimately, we assume that these patterns will create an efficient means of olfactory coding. Knowing that most connections within the antennal lobe are inhibitory, we have tested three alternatives: connections are random, connections are spatially dictated by the neighborhood relationship of glomeruli, or connections are functionally dictated by the response profiles of the connected glomeruli. We found that the functional arrangement best explains the observed data.

The group is currently split with a lab in Europe (Berlin) and one in Riverside. In Berlin, research is done by 4 Ph.D.

students, 2 research assistants, and 2 student assistants. In Riverside, **Rick Vetter** (SRA) is studying olfactory processing in honeybee projection neurons, and **Amy Sage** (student assistant) develops techniques to study olfactory processing in moths, in collaboration with **Kris Justus** and **Ring Cardé** (Entomology, UCR). Computational models are developed in collaboration with **Stefano Lonardi** (Computer Science, UCR). The lab in Berlin will be transferred to Riverside as the students complete their studies, with the last student due to finish in October 2005.

Insects rely heavily on their olfactory sense. Understanding how odors are encoded in their brain will allow us to develop better and environmentally safer approaches to controlling pests, as well as promoting beneficial insects. Furthermore, due to the fundamental similarity of olfactory systems across phyla, these studies help understanding our own sense of smell.

Giovanni Galizia joined the department in January 2003 as an Associate Professor. His Ph.D. is from Cambridge University (UK) and his undergraduate, postdoctoral and Assistant Professor work was - among other places - at the Free University of Berlin.

HONORS AND AWARDS

The Academic Senate has selected **Brian Federici** as a 2004 Faculty Research Lecturer and **Tim Paine** has received the Distinguished Teaching award for 2004. The Distinguished Teaching Award and the Faculty Research Award are the top honors awarded annually by the Academic Senate. **Jeremy Allison** has been awarded a \$300 Graduate Dean's dissertation Research Grant and **Apostolos Kapranos** has been awarded a \$500 Graduate Dean's dissertation Research Grant. **Keith Willingham**, Director of the Technical and Training division at Western Exterminator Company, presented the Karl Strom scholarships to graduate students **Dong-Hwan Choe**, **James Keenan**, **Raj Saran**, and **Andrew Soeprono**. The Carl Strom/Western Exterminator Scholarship is an ongoing fund to support both graduate and undergraduate studies relative to urban pest management.

ALUMNUS FEATURE

By Diana Six

I was one of those people who always knew *deep down* that she wanted to be a scientist. As a kid I had a bug AND a fungus collection. I spent days taking detailed notes on sowbug behavior, mapping out trap-door spider lairs, and testing the ability of green persimmons to preserve mushroom fruiting bodies. After begging for a microscope for several Christmases (and receiving only Barbies and BB guns!!!) I finally received one and spent months living in the world of pond water from which I only reluctantly returned to deal with the more mundane aspects of life. I had a large "school" of "wrigglers" as pets in a big jar for a brief time until our house mysteriously filled up with mosquitoes and I was forever banned from keeping pets. While friends swooned over Capt. Kirk and Davy Jones, I swooned over Spock (oh, what intellect!!) and The Professor on Gilligan's Island (oh, what science!!). However, as I grew older, I drifted away from my dreams, and I eventually dropped out of high school. A college education was not a concept I understood (my mother barely finished high school, my father dropped out at the 4th grade).

Eventually, I earned my high school diploma and then timidly entered college only to experience the incredible mentoring of the biology faculty at Chaffey Community College. All the passion I once had for learning returned with a vengeance. I completed an associate's degree in microbiology (specializing on fungi and lichens) at Chaffey, and then shortly thereafter, completed a bachelor's degree in agricultural biology (entomology/ plant pathology) at Cal Poly, Pomona. I then applied to UCR and worked with Brad Mullens on the use of a fungal entomopathogen for managing houseflies. After completing my master's degree with Brad, I began work with Tim Paine on bark beetle-fungus symbioses. These symbioses turned out to be the passion of my life and I have worked on them ever since. With Tim's great guidance, special sage words from John Menge (I took every class on fungi he offered at UCR and then begged for more), great conversations with Dan Hare (lessons on "the big picture"), and help from many others at UCR, my future began to take shape.

After completing my dissertation, I left Riverside for a postdoc with Don Dahlsten (the great Duck!) at UC, Berkeley, working on the chemical ecology of the natural enemies of bark beetles. However, within a few months, I

was hired at the University of Montana, Missoula, where I started as a tenure track assistant professor of forest entomology/pathology in late 1997. I am now a tenured associate professor.

In the 6.5 years I have been at UM, I have advised 11 graduate students, been awarded 4.6 million dollars in grants, and been involved in collaborative projects in 7 countries. I currently have 12 ongoing research projects in areas including bark beetle-fire interactions, nutritional and developmental ecology of bark beetle-fungus symbioses,



the use of entomopathogens to manage bark beetles, multitrophic-level effects of invasive plants on savanna communities, and white pine blister rust-bark beetle-whitebark pine interactions. The area of research I am personally most interested in is the evolution of insect-fungus symbioses, including the effects and maintenance of cheaters in these systems, and how high levels of horizontal transmission can occur in symbiotic systems that exhibit parallel cladogenesis. This coming year I will spend much of my sabbatical assignment

(yippee!) in South Africa working with Mike Wingfield investigating some of these questions.

At UM I typically teach two classes a semester. Courses include Forest Entomology, Forest Insects and Disease, Biological Control, Research Methods, Careers in Natural Resources, and Insect-Fungus Interactions. It's a great place to teach with an incredible nearby outdoor laboratory called the Rocky Mountains!

I wear a few additional hats beyond that of teacher and researcher. One of these hats includes my responsibilities as a PI on a NSF ADVANCE institutional transformation grant designed to develop UM as a model for rural universities working to increase the participation of women in science. One of my favorite roles in this program was to develop, and now to direct, the new Mentoring Program for Women in Science (designed for both faculty and graduate students). Without the incredible mentoring I received as a student I would never be where I am today – this program provides me with the opportunity to see that others also receive such support.

In my free time, I enjoy fly fishing, fly tying, learning Spanish, hiking, reading really bad mystery novels, and making beer and bread from bark beetle-associated yeasts.

ASSEMBLING THE TREE OF LIFE FOR HYMENOPTERA



The National Science Foundation (NSF) has begun sponsoring an initiative to develop a phylogeny or 'Tree of Life' for all organisms. At UC Riverside, **John Heraty's** lab has become part of a 5

year, 3 million dollar proposal to assemble a phylogeny for Hymenoptera. This is a collaborative effort with the American Museum of Natural History, The University of Kentucky, The University of Kansas and Florida State University. Also, numerous collaborators worldwide are associated with different aspects of this study. The goal is to develop a database of morphological and molecular characters that will be used for a phylogenetic analysis of all of the families, subfamilies and tribes of Hymenoptera. The UC Riverside group will focus on the superfamilies Chalcidoidea and Mymarommatoidea. Chalcidoidea are by far one of the largest and most problematic groups within Hymenoptera, with more than 89 subfamilies, 2,000 genera and an estimated 400,000 species. **David Hawks** (SRA), **James Munro**, **Albert Owen** and **Jeremiah George** (Ph.D. students), **Jung-Wook Kim** (Ph.D. graduated) and **Andy Carmichael** (MSc student) have already developed a molecular phylogeny for almost 600 species with an emphasis on the Trichogrammatidae, Aphelinidae and Eucharitidae. **Roger Burks** (Ph.D. student) is adding substantial new data for Pteromalidae and related chalcids. **Matt Buffington** (Ph.D. student) has helped to develop a morphological web-based image-management system that currently holds more than 5,000 Scanning Electron Micrographs and digital images for use in several laboratories around the world. **Johan Liljeblad** has just joined the Heraty lab as a postdoctoral researcher to assemble the morphological character matrix. In a closely related project, Jeremiah George (Ph.D. student) will be working with the **John Pinto** lab to develop a morphological phylogeny of the Trichogrammatidae and related Chalcidoidea. Looking at the entire superfamily, and Hymenoptera in general, is going to be an exciting adventure, with results that will have significant impact on our knowledge of the behavior and evolution of parasitic and predatory wasps. This endeavor also fits well with the tradition of excellence in research on Chalcidoidea at Riverside, which currently holds one of the largest and best curated collections of Hymenoptera in the world, thanks to the efforts of **Serguei Triapitsyn** (principal scientist and specialist on Mymaridae) and **Doug Yanega** (curator and bee specialist).

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