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ChemoSense

EDITORIAL

The start of something big

By Graham Bell
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Editor of the 33rd edition of *ChemoSense*

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Evolution of Taste: From Single Cells to Taste Buds

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This work is a synopsis of the keynote presentation delivered at the meeting of AACSS at Heron Island in Dec. 2005. The work is dedicated to the memory of Bets Rasmussen, one of the attendees, who succumbed to cancer, diagnosed after her return home following the meeting.

This brief review will examine the world of taste from an evolutionary perspective. First, it is necessary to define what the word "taste" means when applied to human and non-human organisms. This will be followed by a comparison of chemosensory organs that serve taste-like functions in invertebrate and vertebrate forms, ending with a consideration of when during phylogeny taste buds evolved and what distinguishes them from other chemosensory end-organs. A more complete treatment of this subject appears in Finger (2006).

The word "taste" is used conversationally to designate oral sensations associated with substances in the oral cavity. This often includes thermal and tactile sensations as well as chemosensory modalities. In a biomedical context, however, it is more useful to define "taste" as being a *special* chemical sense, in contradistinction to *general* chemical sensitivity of all epithelial surfaces. The term "special" denotes

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Evolution of Taste: From Single Cells to Taste Buds
continued

systems with specialized sensory end-organs in contradistinction to free nerve endings.

For humans, most authors now agree that taste sensations are limited to sweet, sour, bitter, salty and umami. While this formulation works well in describing human experience, it is not always obvious how the term "taste" should be applied to other organisms. By analogy we often extend our experiences to embrace the behaviors of other animals, e.g. we see a monkey eating a banana and assume that the monkey's experience of taste is similar to our own. While this probably is not unreasonable for a closely-related mammal such as a monkey, our assumptions of similarity are less obviously true, if not downright misleading when applied to quite divergent species such as a fruit fly. Is the fruit fly's experience of sugar at all similar to our own experience of sugar?

What is taste?

In humans, taste describes chemically-induced sensations mediated by taste buds. By definition, this excludes sensations of texture, temperature or pressure arising from the oral cavity. It similarly excludes chemically-induced sensations by various compounds such as hot peppers and mint (e.g. hot or cold) due to activation of Trp channels on epithelial free nerve endings or non-specialized epithelial cells. In other words, "taste" denotes sensations arising from taste buds. We use our sense of taste in a feeding-related context - in making the decision as to whether to ingest or reject a potential food item. Accordingly, when applying the term "taste" to non-human animals, it is necessary to identify a specialized chemosensory modality used in the context of feeding.

This definition suffices for humans, and by extension, for other animals with taste buds. But what are the defining features of a taste bud? Taste buds have 3 necessary features: 1) they are small assemblages of modified columnar epithelial cells; 2) they contain multiple receptor cell types; and 3) they form functional contacts with one of the special cranial nerves capable of mediating taste sensations, i.e. facial (CN VII), glossopharyngeal (CN IX) or vagus (CN X) nerves. It is not clear what makes these nerves special, but the ganglion cells for these nerves are unique in arising from epibranchial placodes (Landacre, 1910).

Taste buds occur only within the vertebrate lineage and so any extension of the word "taste" to invertebrates or even invertebrate chordates, is by analogy, and therefore imprecise. In order to extend the definition of "taste" to invertebrates, it is first necessary to delineate the key features that distinguish taste from other modalities in those forms that possess taste buds, i.e. vertebrates. Only then is it possible to apply these principles to identify taste systems in invertebrates.

Humans commonly distinguish between taste and smell according to which vehicle conveys the chemical quality. For humans, tastes come dissolved in a liquid (saliva or water) while odors arrive in a gaseous form. This idea harkens back to experiments done at the outset of the last century when Nagel (as described in Wunder, 1936) reported that he was unable to smell perfume placed in liquid form into his nasal cavity. Yet this vapor-liquid dichotomy fails when applied to aquatic vertebrates such as fishes. All teleost fishes possess both well-developed taste and olfactory systems. A well-differentiated olfactory epithelium is arrayed across an elaborate olfactory organ, while taste buds are present within the oral cavity as well as on the lips and even can be distributed across the body surface. Notably, even when taste buds are spread across the body surface (e.g. catfish have taste buds on their "whiskers", fin and tail), these far-flung taste buds still meet the criterion of being innervated by one of the gustatory nerves; the facial nerve extends a recurrent ramus reaching caudally to the tail. Both odors and tastes for fish are dissolved in water so for fish and other aquatic animals, the medium in which a substance is presented is identical for taste and smell. Thus the medium of stimulus delivery fails as a defining characteristic for taste vs. smell, even within the vertebrate lineage.

Some investigators use the physicochemical nature of the stimulus to define a sensory system: the olfactory system detects volatiles, while a taste system detects hydrophilic stimuli (Bargmann et al, 1993). This scheme for distinguishing taste from smell fails to hold up to scrutiny. In catfish, the olfactory and taste systems respond to nearly identical sets of amino acids (Caprio 1977), all of which are freely soluble in water.

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Evolution of Taste: From Single Cells to Taste Buds
continued

Another common assertion based on human experience is that olfaction operates as a long-distance, low threshold chemoreceptor system, while taste is a high threshold contact system. Certainly for typical terrestrial vertebrates, olfaction operates at a much lower threshold than does taste, but this does not obtain for all vertebrates. For example, the taste system of catfish responds to nM concentrations of amino acids (Kanwal et al 1987) - concentrations not far removed from the olfactory thresholds (Byrd & Caprio, 1982). Thus the relative sensitivity of the two systems is not adequate to distinguish taste from smell. Likewise, in aquatic vertebrates such as catfish, the sense of taste is used to localize a distant food-source without the necessity for direct contact with the food item (Bardach et al. 1967). Thus taste is not necessarily a contact-chemoreceptor system. For both olfaction and taste, while the molecules must contact the sensory end-organ, the ultimate source of the chemical stimulus may be remote.

So if mode of delivery, relative effective concentration, and physicochemical properties all are inadequate to distinguish taste from smell, what then should be taste's defining features? Simply put, taste is a chemosensory system with specialized sensory end-organs and which is used in the context of making decisions as to whether to ingest or reject a potential food item. This definition includes in the taste system, chemosensory end-organs located on non-oral structures as long as the sensory end-organs are used in a feeding context. For example, taste buds situated on the barbels of catfishes are used only to locate food and therefore are considered part of the taste system. Likewise, chemosensory sensilla in flies lie not only in a perioral position, but also along the legs, wing margins and ovipositor (Hallem et al., 2006). While those on the wings and legs are used in a feeding context, the sensilla on the ovipositor are used to select appropriate sites for egg-laying. The sensilla on the mouth parts, legs and wings then, are part of a taste system, while those on the ovipositor are not, since the behavioral context is egg-laying rather than feeding. Some might argue that the sensilla on the ovipositor should be considered "taste" since they express receptors identical to the taste sensilla on the mouth. But similarity in receptor expression cannot define a system. In vertebrates, taste receptors (TR family members) are expressed by non-taste bud chemosensory cells in the respiratory tract (Finger et al. 2003) as well as in the digestive tract (Rozengurt 2006; Dyer et al, 2006; Bezencon et al. 2006).

"Taste"-like Chemoreceptors in Invertebrates

All organisms - whether they be bacteria, plants or animals - respond to chemicals in their environment. So merely responding to chemical nutrients or repellants is not adequate to define a system as "taste". For the purposes of this article, taste must be a chemoreceptor system intimately associated with feeding and mouthparts, hence some level of complexity is necessary before an animal can have a taste-like sensory system. At a minimum, it needs a mouth.

The general plan of organization of the nervous system is different for vertebrates and invertebrates. In invertebrates, epithelial sensory cells are primary sensory cells, i.e. neurons with a sensory dendrite and an axon that transmits information to the central nervous system. In contrast, vertebrates possess secondary sensory cells, i.e. epithelial receptor cells (e.g. hair cells, taste buds) which lack an axon. Rather, these secondary sensory cells form functional contacts with the peripheral process of a ganglion cell which also extends an axon into the CNS. A major exception to this scheme in vertebrates is, of course, the olfactory system, which comprises primary sensory cells similar to those in invertebrates. Nonetheless, with regard to the taste system, the fundamental anatomical organization is different for vertebrates and invertebrates.

Accordingly, the receptor cells for taste in vertebrates are not homologous to and are not phylogenetically related to the receptor cells for the invertebrate taste systems. Indeed, even among invertebrates, the systems referred to as being taste, e.g. in insects and octopus, are not likely to be homologous.

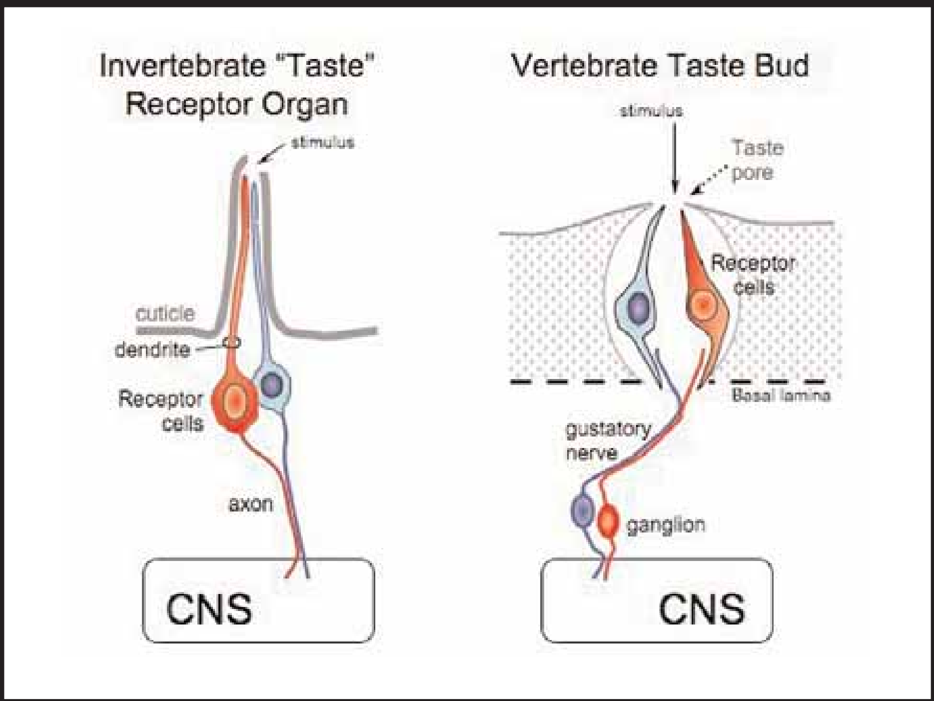

Figure 1: Schematic diagram showing the fundamental differences between chemoreceptor organs of invertebrates (left) and taste buds of vertebrates. The invertebrate receptor organs contain bipolar neurons (primary sensory neurons) with axons extending directly into the central nervous system. In contrast, the receptor cells of taste buds are modified epithelial cells (secondary sensory cells) that lack axons. Rather, the taste bud cells make functional contacts with the peripheral processes of gustatory ganglion cells of the facial, glossopharyngeal or vagus nerves. These ganglion cells also extend a central process to carry taste information into the central nervous system.

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Evolution of Taste: From Single Cells to Taste Buds

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The Phylogenetic Origin of Taste Buds

Taste buds are recognizable in every vertebrate despite differences in the size and detailed morphology of taste buds in the different species (Reutter & Witt, 1993). The common features are: multiple types of modified, elongate (columnar) epithelial cells sitting atop the basal lamina, an apical opening in the surrounding epithelium that permits access of the receptor cells to the external environment, and innervation by sensory processes of the facial, glossopharyngeal or vagus nerves. Taste buds in some species have a highly derived organization; in frogs, taste buds take the form of large (up to 100 um in diameter) taste disks, with a highly stereotyped organization. In contrast, taste buds in birds are relatively small, elongated organs with a long channel connecting the sensory cells to the external environment. In most species, taste buds are ovoid structures, containing 50-150 cells (of which only about half function as receptor cells) embedded in the oral epithelium. They may be situated on raised or sunken papillae, or may be flush with the surrounding epithelium. In all vertebrates examined to date, taste buds contain a cell type that expresses high levels of a specific ectoATPase (Kirino et al 2006). The presence of this enzyme most likely is indicative of the use of ATP as a key neurotransmitter between the taste bud and the gustatory nerves (Finger et al., 2005; Bartel et al. 2006).

Taste buds are present in all extant vertebrates, but is there any indication of a similar organ in the phylogenetically closest relatives? Vertebrates include lampreys, elasmobranchs (sharks, rays, etc.), teleosts (bony fishes) amphibia, and the amniote vertebrates (reptiles, birds, mammals). All have easily recognized taste buds. The closest sister-group to these vertebrates include the hagfish. Hagfish are craniate chordates and have been grouped either with the rest of the vertebrates, or outside of the vertebrates, as the closest chordate (see Fig. 2). Taste buds have not been identified in hagfishes studied to date (Braun, 1996, 1998; Finger 2006). Hagfish do possess two cutaneous chemosensory systems that may or may not be related to taste. The first is a system of solitary chemosensory cells (SCCs) scattered throughout the epidermis and mucosal linings of the nasal and oropharyngeal cavities. Such SCCs are present in all aquatic vertebrates (Whitear, 1992) and a remnant of this ancestral system is present in the nasal cavities of terrestrial vertebrates (Finger et al, 2003). Second, hagfish possess a unique chemoreceptive organ, the Schreiner Organ (Georgieva et al., 1979; Braun, 1996, 1998). This organ contains modified epithelial cells similar in some ways to those in taste buds. Schreiner organs also contain multiple cell types, as do taste buds. So why should we not consider Schreiner Organs to be derived or primitive taste buds? First, the

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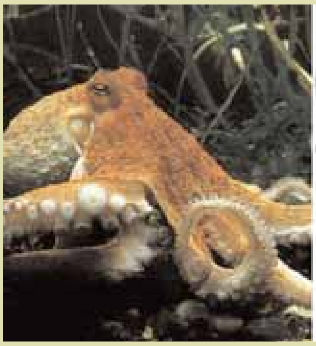
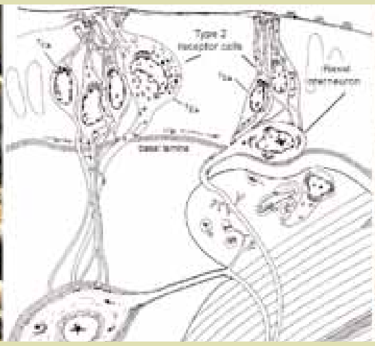
A "tasty" embrace





Left: An octopus, courtesy of U.S. Department of Agriculture, Animal Welfare Information Center, www.nal.usda.gov/awic/pubs/octopus.jpg; Center: Complex structural organization of the chemoreceptors in an octopus tentacle. Although most of the receptor cells have long axons extending into the CNS, some make contact with subepidermal interneurons. Reprinted with Permission from Graziadei & Gagne, 1976. Copyright: Wiley Press. Right: Photo of Dr. Graziadei, about 1995 by Ray Stanyard, used by permission from Florida State University's *Research in Review Magazine*, www.rinr.fsu.edu/summer95/features/war.html.

Octopuses carry potential prey objects to their mouth using their tentacles. The suckers not only enable the animal to "grasp" objects of varies sizes and shapes, but also permit chemical assessment of the object in question. The chemoreceptors on the tentacles have been described in detail in a series of papers by Pasquale Graziadei and colleagues (1964-1975). (Dr. Graziadei is better known for his elegant studies on the ultrastructure of olfactory epithelium [1970-1996] and its capacity for regeneration).

The chemoreceptors on octopus arms are complex, multicellular sensory organs which include primary sensory neurons as well as basal interneurons (see Figure above). Whether these endorgans should be considered to be part of a "taste" system is unclear.

Chemoreceptors with a similar morphology also are present around the oral opening. The octopus appears to use the tentacle chemoreceptors to orient to a food object just as catfish use the taste buds on their barbells to orient to food in their environment. Despite these similarities between octopus and catfish taste systems, the two systems are not homologous, but have evolved independently. Similarities in the systems are due to convergence, not common origin.

Evolution of Taste: From Single Cells to Taste Buds

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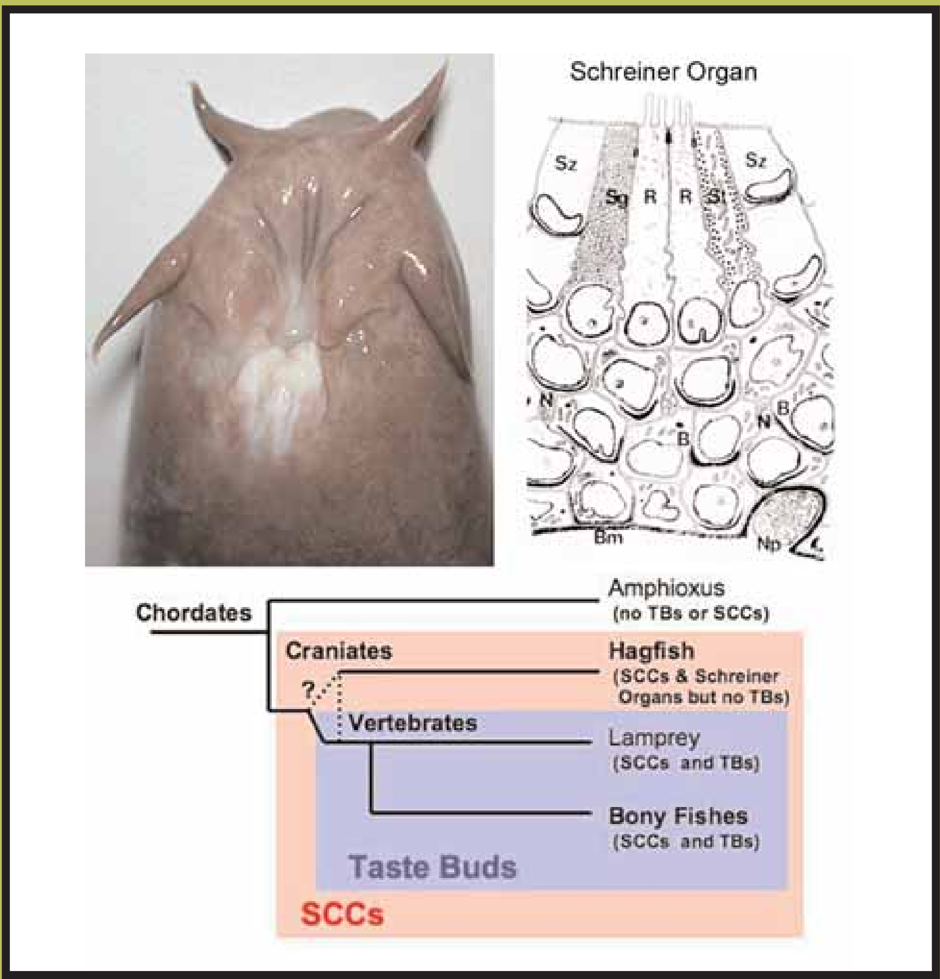

Figure 2: Top Left: Mouth of a Broadgill Hagfish, *Eptatretus cirrhatus*. Schreiner organs, which are similar in some respects to taste buds, occur on the tentacles surrounding the mouth of many hagfish. Photo: Mark McGrouther. Copyright: the Australian Museum.

Top Right: Schreiner Organ. These differ from taste buds in several important ways. Screiner organs do not extend to the basal lamina; they are innervated by non-gustatory nerves, and they do not contain cells expressing ectoATPase. Bm = Basement membrane (Basal lamina); N = nerve process; R = receptor cell. Reprinted with Permission of Blackwell Publishing from: Georgieva et al 1979.

Bottom: Phylogenetic relationships between vertebrates and craniate chordates. The position of hagfish relative to other vertebrates is unclear, but whereas lampreys have taste buds, hagfish do not.

receptor cells of Schreiner organs do not sit on the basal lamina, as do taste cells. Rather the Schreiner organ lies in the upper half of the epithelium. Second, Schreiner organs can be innervated by the trigeminal nerve. In vertebrates, taste buds are always innervated by one of the cranial nerves derived from epibranchial placodes: CN VII (Facial), IX (Glossopharyngeal) or X (vagus). Finally, Schreiner organs exhibit no ectoATPase staining and therefore are unlikely to use ATP as a neurotransmitter, as do vertebrate taste buds. Thus Schreiner organs should be considered to be a derived sensory end-organ peculiar to the hagfishes. These organs may be mere assemblies of solitary SCCs along with some non-sensory supporting cells (Braun, 1996; Finger 2006).

The next closest relatives to the craniate chordates are tunicates and lancelets (amphioxus). These primitive chordates have a dorsal nerve cord and pharyngeal arches, but lack the neural crest that typifies craniates. While these primitive chordates have primary sensory cells that appear to be chemosensory (i.e. cells with cilia and a centrally-directed axon), none have anything remotely resembling a taste bud. The tunicates (e.g. *Ciona*) have secondary sensory cells (lacking an axon, like SCCs, taste buds and hair cells), but these appear to be similar to hair cells rather than SCCs or taste buds (Mackie & Burighel 2005). Similarly, hagfish have well formed seconday sensory cells for the hair cell sensory sytems (e.g. hair cells), but lack taste buds. Taste buds, then, appear only in the vertebrates. The origin of the taste buds in the vertebrate lineage may be related to the appearance in this group of epibranchial placodes which give rise to the gustatory ganglia (Landacre, 1910).

In summary, then, taste buds are present in all vertebrates and constitute an easily recognized taste modality in this group. No other animals have taste buds as defined by anatomical organization (specialized epithelial end-organ innervated by epibranchial nerves) and use (feeding). In comparing the vertebrate taste system to *analogous* systems in invertebrates, some commonalities of organization can be discerned, but these commonalities are attributable to convergence rather than common phyletic origin ■

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NEWS

Bees, Brains, and Robots

In 2004, an astonishing finding published in *Nature* made the news: Judith Reinhard and Mandyam Srinivasan from the Australian National University demonstrated that honeybees have a little Proust in them: when a bee smelled a familiar scent in the hive, it triggered memory recall of the food source associated with the scent, and induced the bee to return to the site.

The honeybee's amazing olfactory learning capacity has been known for centuries (Fig. 1). But what we still do not know is, how it really works: How do honeybees make sense of the countless and chemically complex scents in their environment? Which of the different components in the scent bouquet of a flower do they learn and which do they ignore? How is the amazing chemosensory capacity of bees reflected in the genetic make up of their olfactory receptors?

These are just some of the questions the new CSIRO Flagship Collaborative Research Cluster "Olfactory Pattern Recognition" will be investigating in the next years. Professor Mandyam Srinivasan, or 'Srini' as he is known to friends and colleagues, is the leader of the cluster and

Fig. 1: The honeybee's amazing olfactory learning capacity has been known for centuries

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NEWS

Bees, Brains, and Robots continued

will tackle the above questions together with his colleagues Dr Judith Reinhard and Dr Charles Claudianos (Fig. 2). The research cluster also includes scientists from the School of Biochemistry and Molecular Biology, ANU (Dr Carolyn Behm, Dr Ulrike Mathesius), who are studying chemoreception in nematodes, and scientists from Monash University (Dr Coral Warr, Dr Marien DeBruyne), who are investigating olfactory signal transduction in the fruit fly. Dr Stephen Trowell and Dr Sylwester Chyb from CSIRO Entomology are the CSIRO counterparts of this multi-institute collaboration. The aim is to understand how invertebrates sniff and smell the world, and implement these discoveries in an electronic nose specifically designed to detect subtle differences in grape and wine aromas.

But bees do not only have a superior sense of smell, they also baffle us with their cognitive capacities, which are surprisingly sophisticated considering their brain is the size of a sesame seed. Srini, Charles and Judith are planning an innovative study, digging deep into the honeybee brain: they will probe the bees' ability to feel pain and emotion. They also hope to unravel some of the neural and molecular mechanisms that underlie sensory perception, learning and memory in the honeybee. The recent publication of the honeybee genome in Nature, which Charles was involved in, provides an unprecedented opportunity to tackle these important questions. This new research will take Srini, Charles and Judith to the prestigious Queensland Brain Institute (QBI) at the University of Queensland, where the team will move to in early 2007. AACSS members Charles and Judith are especially excited about their move, as it

Fig. 2: . Professor Mandyam Srinivasan, with his colleagues Dr Judith Reinhard and Dr Charles Claudianos.

offers a chance to collaborate with Brisbane AACSS scientists Brian Key, James St John and Alan Mackay-Sim, to mention just a few.

And what can bees and brains teach us about robotic engineering? Not much one would think, but there is one extraordinary scientist who successfully amalgamated these research areas. We are talking about Srini, of course. Not only is he an expert on bees and brains, he is also one of the world leaders in insect-inspired robotics. How did all this come about? After starting his scientific career as an engineer in India, Srini moved to Yale in the USA, where he discovered his passion for biology, in particular insect vision. He was introduced to honeybees during a research stay in Switzerland and continued to study them after moving to Australia. Honeybees and their amazing sensory and cognitive capacities have since been the focus of Srini's work. His discoveries on how honeybees use visual information to navigate in cluttered environments, maintain flight speed and accuracy, and manage successful landings have been implemented into small autonomous aircraft, with the aim of designing flying robots with the sensory capacities of insects. In recognition of his outstanding achievements, which include a number of key *Nature* and *Science* publications, Professor Mandyam V. Srinivasan FAA FRS has been awarded the Prime Minister's Prize for Science for 2006.

Congratulations, Srini! Now you know whom to ask should you ever have a question about bees, brains or robots.

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CALL FOR ABSTRACTS

Contributions are invited for oral and poster presentations at the Symposium. Accepted oral presentations will be allocated a 20 minute slot in the final program. Please submit abstracts online at www.pangborn2007.com by 31 January 2007.

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Visit the E-Nose Pty Ltd Booth, No. 238

13-15 April 2007
ISOEN (International Symposium of Olfaction and Electronic Nose)
St Petersburg, Russia
Info: www.isoen.org

25-29 April 2007
AChemS
Sarasota, Florida, USA
Abstract Deadline: early Jan 07
Info: www.achems.org

7-9 June, 2007
"Bacchus at Brock"
International Interdisciplinary Wine Conference
St Catherines, Ontario Canada
Info: www.brocku.ca/bacchus

9-11 July, 2007
39th Annual AIFST Convention
Adelaide Convention Centre
Adelaide South Australia
Info: aifst@aifst.asn.au or www.aifst.asn.au

July 2007
AACSS: 9th Annual Meeting
Adelaide, South Australia
Contact: Stephen.Trowell@csiro.au

12-17 July 2007
IBRO (International Brain Research Organisation)
Melbourne, Australia
Contact: http://www.ibro2007.org

19-23 July 2007
Avian Olfaction Symposium
IBRO Satellite on Avian Brain, Cognition and Behaviour
Heron Island, Queensland, Australia
Info: http://workshops.med.monash.edu.au/birdbehaviour07

28 July - 2 August 2007
The 13th Australian Wine Industry Technology Conference
Adelaide, South Australia
Contact Rae Blair: rae.blair@awitc.com.au

12-16 August 2007
7th Pangborn Sensory Science Symposium Hyatt Regency, Minneapolis, USA
Abstract deadline: 31 January, 2007
Info: www.pangborn2007.com

6-8 May 2008
Enviro 08
Melbourne
Info: rvquitz@bigpond.com

21-25 July 2008
International Symposium on Olfaction and Taste (ISOT)
San Francisco, USA
Now calling for proposals for satellite meetings
Contact Tom Finger: tom.finger@uchsc.edu ■

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