Technical Report

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Insect Sensory Systems Inspired Communications and Computing (I): A Biological Perspective

TR-CS-09-01-2007
University of Idaho, Computer Science Department • September 4, 2007.

Insect Sensory Systems Inspired Communications and Computing (I): A Biological Perspective

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Abstract: Insects are the most successful group of living things in terms of the number of species, the biomass and their extreme survival and reproduction capabilities. Entomological research has revealed that insect sensory systems are crucial for their extremely successful conquering and exploitation of every habitat niche on earth planet. Compared with human beings, insect central nerve system (mainly brain) is extremely primitive and simple both structurally and functionally, and is of minimal learning ability. Faced with these constraints, insects have evolved a set of extremely effective sensory systems with features such as structurally simple (e.g., some sensor receptors are single cells), functionally versatile and powerful, highly distributed, as well as noise and fault tolerant, etc. As a result, in recent years, significant advances in this interdisciplinary field have been achieved. However, we believe that the potential of this field is far from being fully recognized. In particular, the contrasting similarity between the ubiquitous existences of insect sensory networks in nature and the ideal of pervasive computing has received little attention. This article attempts to introduce engineers and computer scientists to a comprehensive view of insect sensor systems, identifying areas that have high potential for new directions. It attempts to point the reader directly to the state-of-the-art advances, narrowly guiding though an enormous body of research from the field of insect sensory systems. We hope that this article will lead to new inspirations and research directions in communication and computing systems.

Keywords: Insect Sensory System, Pervasive Computing, Insect Chemosensory System, Neuromorphic Engineering, Infochemicals, Multimodal Sensors Network, Insect Sensory Ecology, Insect-Inspired Agent Computing.

1. Introduction

Lord Avebury's book "On the senses, instincts and intelligence of animals: with special references to insects" published in 1902 seems to be the first monograph on insect sensory system. The monograph touched every aspect of insect sensory systems such as smell, taste, hearing, sight, vision, direction, instincts, even the question whether insects can count (Lubbock 1902).

The extant number of species of insects on earth is estimated between 2-10 millions, and of the about one million scientifically identified animals, 72% are insects (Peters 1988). Insect species outnumber all other organisms combined. So why are there so many insects and why are they so successful in conquering the planet? There are a variety of factors and the following four are among the most frequently cited: (1) the high level of organization of insect sensory and neuromotor systems, (2) the minimal learning capacity and short generation time, (3) the small size, and (4) the nature of the co-evolutionary interactions that involve insects (Peters 1988, Richards and Davies 1977). The first factor is essential and insects are only matched by vertebrates with regard to it. A high level of organization enhances the ability to perceive small environmental differences and react to them. It effectively maximizes the apparent heterogeneity. One natural question is: if insects and vertebrates score equally well in sensory and neuromotor systems, then why are we interested in studying insects for inspiration to engineering problems rather than looking at the extensive biomedical research of human beings? There are several justifications but the main one lies in the simplicity and highly distributed nature of insects sensory systems. Many of the insect sensory receptors are single cells, which are much easier to study and emulate. Furthermore, the highly distributed organization and extreme tolerance to noise and faults of insect sensory systems are highly desirable features for modern communications and computing systems.

With respect to factor (2) above, insects have minimal learning ability and vertebrates are superior without the slightest dispute. However, the minimal learning capability forces insects to depend on instincts that are genetically "programmed". In order to adapt to constantly changing environments, they have to "reprogram", i.e., to change their genetic code rapidly, to adapt to local environment perturbations. Their short lifetimes are actually favorable for evolving the rapid genetic changes (Richards and Davies 1978). Therefore, the deficiency in learning ability forces insects to diverge genetically and evolve more species. When organized (assembled) in populations (of "dumb" individuals) they demonstrate characteristics of complex systems such as self-organization, emergent behavior, and highly distributed organization. This ability to build an adaptable and reliable organization with "dumb" agents is similar to the design goal of wireless sensor networks and ad hoc networks.

The small size mentioned in factor (3) above is an advantage in that it makes them less likely to get extinct than big animals. Insects, as the smallest animals that have wings for flying, have already been studied extensively in mechanical and aerospace engineering. For example, in military applications, insects may be the best models for the MAV (Micro Aerial Vehicle), with magnitudes of centimeters, communicating via wireless ad hoc networks (Ma et al. 2008). With respect to factor (4) above, insects' co-evolution, e.g. with plants, is the most interesting arms race in evolution and has received significant attention in evolutionary computation. Co-evolved interspecies relationships such as parasitoids-host and symbiosis can be modeled by search-game theory (Alpern and Gal. 2003).

Social insects, especially ants, termites and bees, have received significant attention in computer science and have resulted in new concepts like swarm intelligence (Bonabeau et al. 1999, Dorigo and Stützle 2004). However, we believe that social insects as the basis for inspiration to computer science and engineering problems are only a small part of a much larger view. Social insects make up only about 2% of the identified insects species. The majority of insects are not social but still extremely successful in their struggle for living. This suggests that perhaps most sources for potential inspiration have not yet been explored.

To some extent, insect sensory systems assume part of the functions performed by the central nerve systems in their vertebrate counterparts. This means that insect sensory systems perform significant computing and information processing functions. What is even more remarkable is that their chemical sensory systems, which release and use pheromones for intra-specific communications and allelochemicals for inter-specific interactions, essentially form "wireless" communication networks that control and/or regulate their behaviors and many other aspects of their lives. These chemosensory-based communication systems use semiochemicals (also known as infochemicals, a term used for both pheromones and allelochemicals), rather than the radio frequencies, to encode/decode messages. Chemosensory-based communication systems in insect populations are extremely specific (e.g., only perceivable by individuals of the same species), reliable and robust. These are the very characteristics we desire for our communication and computing systems such as wireless sensor network and pervasive computing. However, to date chemosensory-based communication systems have not been explored.

The remaining of the article is organized as follows: section 2 discusses major modalities (types) of insect sensory systems and their integration. Section 3 introduces one of the latest research subjects, insect sensory ecology, which studies how insects use sensory information in their interactions with the environments. This new subject focuses on the adaptive use of sensory stimuli. This is very relevant to issues in pervasive computing such as ambient intelligence. The section 4 concludes with a summary and a discussion on insect-inspired agent computing.

It should be noted that, given the immense volume of research in insect sensory, it is well beyond the possibility of an article of this length to touch all the major research topics in the field. Instead, we introduce the reader to the latest advances in entomology that, in our opinion, are most relevant to communication and computing. We intentionally ignore some topics that have been sufficiently addressed in the literature, e.g. swarm intelligence. Also, while we try to convey the big picture of various insect sensory systems for non-entomologists, our primary effort is focused on providing, what we deem as the potentially most promising and insightful reference points for scientists in communication and computing fields. We frequently cite only one paper when multiple papers from the same author or group could be supplied. Priority is given to the state-of-the-art review papers and research involving mathematical modeling.

2. Sensory Modalities and Multimodal Signal Integration and Behavior

Insects possess all the sensory modalities vertebrates have, despite their nerve system, which has to process stimuli picked up by sensory systems, is very simple compared with that of vertebrates. The major modes of the sensory systems include chemosensory vision, mechanosensation and audition, and olfactory chemosensory. The latter is the most developed. In addition, thermoreception (used by mosquitoes), infrared reception (used by buprestid beetles), and magneto-reception have also been found in some insects.

2.1. Audition/Mechanosensory

It is often difficult to draw the line between hearing (audition) and mechano-sensation, since insects perceive auditory signals via either airborne sounds or substrate-borne vibrations. Insects audition is considered to be much less developed than olfaction and vision because their small size is often considered the major constraint to develop powerful audition systems. However, in many insect species, highly specialized auditory systems have been evolved to extract relevant signals form an acoustically noisy medium (Larsen and Svensson 2005). There has been enormous research on insect sounds in the past 50 to 60 years. This trend has been accelerating in recent years with the help of modern digital technology to record and process insect acoustical signals. These latest advances, as shown in Drosopoulos and Claridge (2006), seem to suggest that we may have underestimated the insect audition capability. Insect sounds are often called "songs" which are simply noises to most human ears. Recent studies have detected some unusually low frequency vibration signals transmitted via substrate, which are often not detectable by the human ear without amplifications. Low frequencies are often only usable for insects when the communication is via substrate vibration. Nevertheless, most insects, when engaged in aerial communication, are forced to use relatively high frequency sound and even ultrasound, mainly due to their small body size (Claridge 2006).

Studies of insect sound and communication often focus on sexual behavior in mate searching, recognition and courtship. One very interesting research topic is the modeling of optimal host-searching strategies of parasitoids who try to locate and oviposit their eggs into their hosts — leaf-miner insects who themselves "hide" inside the tunnels within a plant leaf. The interaction between a leaf-miner and its parasitoid enemy involves wave vibrations and their perception. Their hide-and-seek game can be *played* up to 20 minutes. The leaf-miner--parasitoid system was formulated as the "princess-monster" search game and studied thoroughly (Djemai and Meyhöfer et al. 2000, 2001, Alpern and Gal 2003, Casas and Magal 2006).

The songs of grasshoppers are produced by a rhythmic movement of their hind legs against the forewings. Herz and Benda et al. (2005) presented the mathematical modeling framework for neural coding in insect acoustic communications using *Locusta migratoria* as the model insect. A single sensory neuron is modeled as a linear filter (L), which acts on the stimulus in the time domain, followed by a static nonlinear (NL) cascade. More complex transduction processes can be modeled as combinations of elementary NL cascades. Phenomenological differential equation systems are derived to model the output driven adaptation. The renewal stochastic process is used to derive the stochastic version of the phenomenological model. Based on the single neuron model, Herz and Benda et al. (2005) further build the signal-processing model with information theory and the standard signal processing technology in electronic engineering. Information-theoretic adaptive sampling plays an important role for this research (Machens 2002, Herz and Benda et al. 2005). Perhaps the most interesting inspiration from this research is the implication that the small insect neural systems are able to perform non-trivial time-multiplexing operations and the required complex computations.

2.2. Vision

Most insects possess a pair of large compound eyes, often occupying significant realty of their head. Often three single-lens eyes, known as ocelli, also exist on the upper part of the head, between the compounded eyes. Compounded eyes are made of hundreds or even many thousands of somewhat identical "simple eyes", or ommatidia. It is still a mystery why insects have evolved compound eyes since compound eyes seem hopelessly inefficient in terms of spatial resolution, compared with single lens eyes. One conjecture is that they are simply stuck with their basic ancestral design. In other words, there is no sufficient evolutionary selection pressure to transit from compound eyes to single-lens eyes (Larsson and Svensson 2005). One particular explanation is that the compound eyes may be inhomogeneous, that some areas are of higher resolution. This may compensate to some degree for the overall low image resolution. Most insects have tri-chromatic color vision with photoreceptors most sensitive to ultra-violet, blue and green parts of the spectrum. On the other hand, in spite of the low spatial resolution of insect's compound eyes, some day-flying flies and bees have very high time resolutions (up to 400 frames per second). This is why flies are so agile and fast when one tries to catch them (Rind 2005).

The most intensively studied insect compound eye is that of the fruit fly (*Drosophila*). It is generally agreed that butterflies and moths have excellent color vision among insects. However, studies of color-driven behavior supported by butterfly eyes are still very preliminary. With respect to inspiration for engineers, the study of the widespread heterogeneity in insect compound eyes may be most promising.

The case study of neural computations in the blowfly conducted by Egelhaaf and Grewe et al. 2005 focused on the reliability of neuron coding. They consider that, since the individual neuron in compounded eyes has such high response variability, a population of neurons has to be quantified to study the neural response. Information theory is used to analyze how much information about the stimulus is encoded by a neuron. Information theory implies that the more states a stimulus assumes, the more information it contains. In addition, the information content of a stimulus is also influenced by the probability distribution of the states. Therefore, the information conveyed by a neuron is determined by the probability distribution of the neural response levels. Bayes theorem is then applied to obtain response of the neuron population. The complex spatial-temporal properties of natural image sequences and the resulting complex time-dependent neural response, as well as the variability of individual neuron, in insect nerve systems may have high significance to machine learning and grid computing.

Despite of the limited understanding of insect's vision, the hope and the potential stake in the field is very high. Scientists hope that the understanding of computational design principles of insect brains down to level of neurons and neural networks will not only answer interesting science questions, but also provide practical applications in robots and autonomous manmade flying machines. Modeling has been and will continue to play a crucial role in establishing neural computational principles of insect vision and their applications in engineered systems (Egelhaaf and Grewe et al. 2005).

One field that has made enormous progress in recent years is the motion detection of insect eyes and their applications to bio-inspired robot sensors. A reason for the advancement is that motion-detection neurons are some of the largest in insect vision systems and easy to observe (Rind 2005). Rind (2005) summarized three types of contributions where engineered vision systems are based on insect vision system: (1) Bio-inspired circuits embedded in the control structure of mobile robots. Examples are the Lobula Giant Movement Detector (LGMD) for collision detection based on locust eyes (Blanchard et al. 2000, Rind 2002) and flying motion detectors (Franceshini 1992). (2) Neuromorphic chips based on fly eyes (Harrison 2000) and VLSI retinal circuits (Liu 2000), and (3) bio-inspired behavioral strategies (Srinivasan et al 2001). In these insect-eye-inspired designs, the goal has been to make fast, robust, lightweight and low-power vision systems. Another feature is that analog-VLSI has been the dominant choice in insect-vision-based chips. Ruffer and Franceschini (2003) have designed neuromorphic eyes for a mini-UAV with eye weights of only 0.8g and a weight of only 100g for the entire rotorcraft. Tests reveal that these artificial vision chips, (even the most flexible analog-VLSI fly eye), still have significant gaps with real insect visions systems upon which the chips are based. This indicates that a better understanding of insect eye motion detection has to be gained to make further breakthroughs (Rind 2005).

2.3 Gustation

Gustation, contact chemosensory and taste are generally interchangeable in entomology. Taste takes on a crucial role in finding the right kinds of food in sufficient quantity. However, insects also must "remember" and "recognize" tastes to avoid unpleasant or poisonous food. What may be different from many other animals is that taste also plays an important role in insect oviposition behavior and their choices of oviposition sites. Insect gustation has been studied in a wide variety of insects, including flies, mosquitoes, honey bees, moths, locusts, leafhoppers, aphids, and butterflies (Hallem and Dahanukar et al. 2006). They are important for locating high quality food and avoiding poisons. Insect taste receptors are located on various body parts, including mouthparts and tarsi. Most research has used *Drosphila melanogaster* as the model system. Bioinformatic approaches such as taste receptor gene analysis has been the focus of the *Drosophila* studies. However, little is known about the essential mechanisms of taste perception in insects (Perry & Dahanukar et al. 2005). The chemosensory systems of insects are based on both gustatory and olfactory. In fact, insects have the most advanced olfactory system, which makes their comparative research very valuable.

One of the major motivations for studying insect taste is the hope that the relative simple insect nerve system, which is amenable to rigorous analysis, will provide insights to the research of vertebrates taste (Newland 2005). Taste is very notorious difficult to study; this has been exhibited by the status of research into vertebrate taste. After near a half century of research, scientists still do not have full understanding of how taste is encoded in vertebrate brains. For example, in vertebrate research, the debates of two major hypotheses on taste encoding are far from settled. One of the hypotheses, known as *population code* or *across-fiber pattern*, assumes that the range of chemicals that an individual chemosensory neuron responds to is variable among the population's individuals. This is similar to the vision neuron coding we discussed earlier. The alternative hypothesis, referred to as *labeled-line code theory*, assumes that the sensory neurons are grouped into specific categories, each of which encodes a specific taste quality without overlap in selectivity. With either population code or labeled-line code theory, mathematical modeling plays a significant role in (1) studying the chemosensory communication mechanisms and (2) designing engineered systems. It seems that mathematical modeling in insect chemosensory is even behind its peer field such as insect visual driven communication. The above two hypotheses for taste chemosensory encoding have been extended to olfactory encoding and will be revisited in the next section.

2.4. Olfaction

Olfaction (smell or odor) and gustation (taste) both belong to chemosensory and the difference lies in the non-contact vs. contact sensation. Insects rely on olfactory stimuli for their reproduction and survival. As we mentioned previously, insect chemosensory system is considered the most contributing factor for the extreme success in their evolution. The antenna and, to a less extent, the maxillary palms, are the most important olfactory apparatuses in insects. One of the biggest challenges in studying insect chemosensory is the potentially "infinite" number of chemicals, known as semiochemicals or infochemicals. Each type of the semiochemicals is unique in terms of its ethological effects (Larsson and Svensson 2005).

Semiochemicals can be classified into two types, i.e. pheromones and allelochemicals. Pheromones are used for intra-specific communications, whereas allelochemicals are used for inter-specific interactions. Pheromones are further divided, according to their functionalities, such as sex-, alarm-and aggregation-pheromones; they are generally beneficial to both emitters and receivers. Allelochemicals are divided into kairomones, allomones and synomones in terms of their benefits to receivers, releasers, and both, respectively. What complicates the classification is that the same chemical can be classified into more than one type when more than two parties are involved.

One of the best-known pheromone inspired computing scheme is swarm intelligence based on the ant aggregation pheromones. Several monographs have been published on the topic, including Bonabeau et al. 1999, Dorigo and Stützle 2004. We believe that much of the chemosensory communication mediated by semiochemicals is still largely unexplored, given its dominant role for the survival and reproduction of insects.

The crucial importance of olfactory communications to insects cannot be overemphasized. For example, males often locate females by following the smell of female-released sex pheromones. Furthermore, females may depend on host-emitted cues to determine where to lay their eggs. Smell cues also play a crucial role in locating food sources, such as blood meals. Olfactory research is therefore the central topic for understanding insect neuroethology. Started in the 1950s, scientists have conducted extensive studies of insect peripheral olfactory systems (mainly antenna). Recent studies have focused on the next level, the primary olfactory center in the insect brain, known as antennal lobe (AL). The electroantennogram (EAG), pioneered by Schneider in the 1950s, is still one of the most important techniques for studying insect olfaction (Ignell and Hansson 2005). The antennal lobe occupies significant percentage of insect brain and is unique to insect. The pair of AL receives signals from several hundreds of thousands of peripheral olfactory neural receptors (ONR) located on the insect's antenna, and acts as the first level of signal integration in an insect brain. AL is very similar to dedicated processors for crucial peripherals in computer systems, which further highlights the crucial importance of the olfactory sensory of insects. The complex signal integration and transformation conducted by AL and the interactions with higher olfactory centers in the insect brain are still not well understood.

There are two basic concepts in the olfactory coding of odor quality, which receive a growing consensus among scientists. The first concept suggests that discrimination of odors depends on a combinatorial coding process, involving the ensemble activity of a diverse array of projection neurons (PN) in the AL. One implication of this concept is that neither labeled lines nor across-fiber patterns (briefly discussed in the taste section) by themselves are able to explain the encoding process fully. Instead, a hybrid coding strategy of both is suggested (Christiensen and White 2000, Ignell and Hansson 2005). The second concept suggests that synchronous firing among PN is a key mechanism for strengthening the neural representation of odors in the brain.

It has been suggested that odor intensity in honeybees is processed by distinct neuronal subsystem of PNs. This means that encoding of information is performed by different parallel neuronal pathways responsible for intensity-coding (odor concentration or quantity) and quality-coding (as discussed above), respectively. Quality coding is concentration-invariant. Although these separated pathways or networks for quality and quantity encoding seem to be hard to find in engineered systems, its appeal is obvious. Especially the concentration-invariant mechanisms are very inspiring. In the past few years, several strategies for concentration-invariant coding have been proposed. In several experiments, scientists found that different odors evoke activity in different subsets of glomeruli, and the particular subset of glomeruli is relatively consistent across stimulus concentrations. Glomeruli are the functional units of the AL. Their numbers differ widely among insects. Glomeruli are different in shape and size, but within a species, their spatial arrangement is reproducible.

The other proposal suggests that odor identity in insects and vertebrates can be encoded by specific spatial-temporal activity patterns of PN assemblies over time. This model implies that odor representation is a multidimensional vector of PN states that evolve over the duration of stimuli. A problem of the model is the requirement for a relatively long duration of the stimuli, which in some scenarios is not the case. One hypothesis to address this "duration for evolving" is that the representations do not evolve and instead, they are dictated by the temporal pattern of stimuli. This brings up another very important research topic, i.e., time as a factor in AL processing, since brief intermittent stimulation is crucial for odor discrimination in many insects

(Ignell and Hansson 2005). Beyond AL, our understanding of the higher brain area in charge of olfactory processing is very limited.

Before concluding this section, we would like to briefly mention two recent advances in the techniques for studying insect olfactory systems. Whereas the electroantennogram has been used for more than half a century in insect olfactory studies, two categories of new technologies have been developed which significantly contribute to the accelerating advances in the field. One category is optical imaging, which measure neural activity using light by introducing activity-dependent dyes into the neurons. The dyes (which are often genetically engineered proteins) change their optical properties as a function of metabolic variables such as cell membrane potential, or concentration of certain molecules. Mathematical modeling and statistical analysis of the data obtained from optical imaging is a very important aspect of the methods. The appealing of optical imaging for insect physiology analysis lies in its ability to combine spatial analysis of identified units and the diversity of physiological mechanisms analyzed in an in vivo scenario. It is very suitable for insects, for which *in vivo* physiology is much easier to conduct than in vertebrate physiology (Galizia & Vetter 2005).

The second category of techniques, which is getting popularity in insect physiology, is the multi-channel neural ensemble recording (MNER). This technique was developed in the last few years to address one of the fundamental tenets of neurobiology that complex signals in the brain are often represented across distributed populations of highly interconnected neurons. The MNER technique allows the simultaneous recording from many neurons across the brain (Pawlowski and Christensen et al. 2005). Using simple wire electrodes that are inserted into the cortex has evolved in nearly a century. The latest "wire" used in entomology is the silicon-based MNER arrays. These new-generation of "wire" is actually microprocessor controlled (DSP or PC) instrument with comprehensive software support for data acquisition and analysis. Some of the systems even have interfaces with standard software such as MATLAB (Pawlowski and Christensen et al. 2005).

2.5. Multimodal signal integration and behavior

Animals have multiple sensory channels that receive signals from the environment and then convert them to adaptive behaviors and memories. Scientists have obtained significant understanding of how information is encoded within single sensory channel, e.g. sight, hearing, taste and smell. Still little is known about specific interactions between the different sensory modalities. These interactions are actually fundamental because the different sensory channels are evolved to work in coordination to handle parallel stimulations to multiple sensory channels (Homberg 2005). The advantages of using insects as target animals for studying multimodal interactions lie in: (1) the possibility to identify individual nerve cells responsible for the functionalities under various contextual conditions; (2) the feasibility to study the physiology of identified neurons naturally.

It has been demonstrated that the insect brain plays a significant role in multi-sensory signal integration. Multimodal sensory processing serves several functions such as object identifications, goal-directed movement, flight control, learning and memory. Most of research supports the notion that a particular neuron responds to multiple sensory modalities in insects. This ability to handle multiple modality information is very desirable in engineering.

3. Insect Sensory Ecology

Insect sensory ecology is a very recent term, although the problem domain it addresses has been studied for a long time. It is defined as the study of how insects use sensory information in their interactions with the environment. Sensory ecology is broader than already established chemical ecology, since it also implicates physics, chemistry, physiology behind the generation and perception of stimuli. Its focus is on the adaptive use of sensory stimuli. It is generally recognized that insects' adaptations are imperfect compromises between conflicting selective pressures working within the physical constraints and the evolutionary history of an insect species (Larsen and Svensson 2005).

3.1. Signal Detection

Insects depend on sensor receptors to detect stimuli. It has been established that insect sensory receptors often operate at their maximum theoretical sensitivity, e.g. the detections of single photons or odor molecules have been documented. However, the absolute sensitivity, although certainly appealing for engineering design to improve sensor sensitivity, is often not the dominant adaptive factor. It turns out that insects have evolved very diverse adaptive strategies to improve signal/noise ratios in their sensory systems. One common strategy to filter out noise in low intensity signals is to use the so-called summation, i.e., averaging many neurons over extended time periods to obtain a more reliable estimation. The summation over space is demonstrated by some male moths with enlarged antenna covered with tens of thousands of chemoreceptor tuned to detect specific components in female-released sex pheromone blends. Another interesting strategy to improve signal/noise ration is to detect and amplify primarily those features of the signals that are of particular interests, they are termed as "feature detectors" or "matched filters" in the insect sensory research literatures.

Although the number of insect species exceeds the total species number of all other living things combined, they exhibit remarkable niche specialization. For example, vast majority of insects feed on single or a few related host species. One of the explanations for the high specialization is sensory limitation. The justification for the hypothesis is that selecting a combination of a few predictable stimuli that indicate essential resources (such as hosts) with high certainty, promotes the sensory systems to maximize the efficiency of resource utilization. The signal specialization may also be helpful for avoiding catastrophic mistakes (Bernays 2001, Larsen and Svensson 2005).

3.2 Sensory System Model

To describe the chemical communications of insects the conceptual emitter-medium-receiver model shown in Figure 1 was proposed by Endler (1993). The emitters may be animate or inanimate objects, but usually they refer to the former, e.g. other insects. Whereas this model was developed in the context of chemical communication, the principle seems to hold in communication systems using other types of signals.

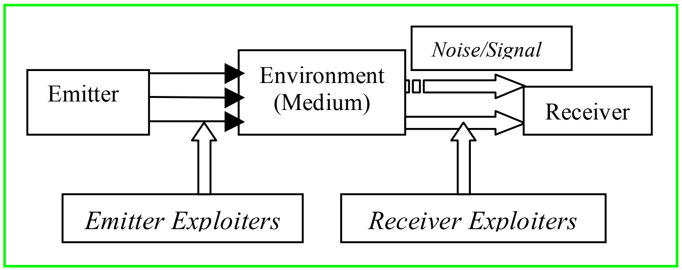

Figure 1: Basic Components of the Emitter-Receiver System (after Endler 1993, Larsson & Svensson 2005).

Most of the signals in insect communication are semiochemicals and the communication medium is generally the "air wave", but also can be water or other substrates. This communication model is very similar to wireless communication in engineering. The model is an extremely simplified view and the intricacies in the insect chemosensory system often surprise researchers. For example, in the 1970s scientists already discovered that there are some insects (such as the clearwing moth in the family of *Sesiidae*) where the male and female communicate by identifying the blend ratios of isomers of sex-pheromone compounds released by females. This means, different species encode their communication channels by manipulating the ratios of isomer blends, although the same pheromone compounds may also be used by their relative species. This mechanism is used in "long-range" communications between male and female clearwing moths before they enter the same courtship area (Greenfield and Karandinos 1979). Reproductive isolation is essential for biological species (interspecies mating is harmful and "prohibited" in higher animals and species). The fact that clearwing moths depend on encoding the isomer blends of sex-pheromones to ensure that only males of the same species can decode the signals transmitted by the female-released pheromone is a proof for the reliability of the system. However, the communication is sufficiently reliable, but not perfect.

In the emitter-receiver model of Figure 1, two forms of exploitations may occur. First, the emitter may be exploited by enemies that are able to decode and locate the signals, e.g. parasitoids and predator. Second, predators acting as impersonators using similar signals may lure the receiver. These exploitations have motivated extensive studies in entomology and pest management on insect semiochemicals, since they provide insect pest control measures safe to the environment and human health. In the context of wireless sensor network, the inspiration may come from the imperfect communication mechanisms that still guarantee the survival of the species (from extinction) in its evolutionary history.

The evolutionary process to adapt to the two aforementioned exploitations is very interesting. Scientists believe that if the interactions are beneficial to both emitter and receiver, true communication often evolves. Specifically, the sender and receiver can agree on a signal and its meaning and evolve to optimize the signal transmission and processing, while excluding unwanted impersonators (Wyatt 2003, Larsson & Svensson 2005). When the interaction is detrimental, the emitter may opt out by so-called crypsis mechanisms with which it reduces or confounds the signal. As a result, the receiver increases its signal processing capacity to better distinguish undesirable signals from adaptive ones.

3.3. Sensory System Cost and Constraints

The energy cost associated with the sensory system of insects is probably much higher than that of vertebrates, given the high ratio of sensory organs to body mass or size. For example, the metabolic energy associated with electrical coding of the compound eyes of the blowfly can reach 10% of the total energy expenditure during flight and 3% during the rest. This is astronomical compared with the eyes of vertebrates. There is little research on how insects optimize the energy consumption of sensory systems. However, it can be expected that they must have evolved intricate strategies and tactics, given the extremely high stake in the overall energy allocation and the crucial importance of their sensory systems (Christensen 2005). Knowledge of how insects optimally allocate energy to their sensory system may provide useful insights for designing energy efficient sensor networks.

4. Epilogue.

From previous brief review, we can see that insect sensory systems, as insects' major peripheral neural systems, possess many delicate mechanisms that are highly inspirational for the engineering design. While in this article, we suggest some of the inspirations in various contexts corresponding to different insect sensory systems, we postpone the comprehensive review of existing insect sensory inspired computing and communication to a follow-up paper (Ma et al. 2008). However, most of the inspirations mentioned here seem not have been explored in engineering yet, mainly because the corresponding entomological research introduced in this article happened only in last few years.

Among the various modalities, it appears that vision and mechanosensory have received most of the attention in engineering. However, we believe that the most advantageous sensory system, from the perspectives of both insect life and engineering science, is the chemosensory system. While biologists have recognized this biological significance, it has not crossed over to the engineering and computing fields. As we have pointed out, the insect sensory system is one of the top four reasons for their extreme success in the nature. In particular, in many insects the chemosensory system is the most important communication systems, which is also used to perceive and adapt to their environments. This kind of mechanism could be very inspirational for new design paradigms for pervasive computing. We also hope that the discussion of the insect sensory ecology, which studies how insects use sensory information in their interactions with the environment, may give insights for the development of new strategies related to environment-aware and adaptive computing.

Finally we would like to point out that agent computing is another field for which the insect model can play a significant inspirational role. The term agent has a very generic interpretation in computer science. An agent can be considered as a computational system that senses and responds to its environment intelligently based on its goals. Quite a few models were proposed to describe the structure and function of an agent. One of the most popular is the insect-inspired model (Borghoff and Schlichter, 2000) shown in Figure 2. In the depicted insect-inspired agent model, the agent can communicate with other agents via the environment or communication channels such as described in Figure 1. The head stores, manages and controls the cooperation abilities and schemes. It also possesses other agents' skills, the current states, and communication protocols, etc. The actual agent functionality is built in the body. Borghoff and Schlichter also reviewed the distributed algorithms for agent-based computing.

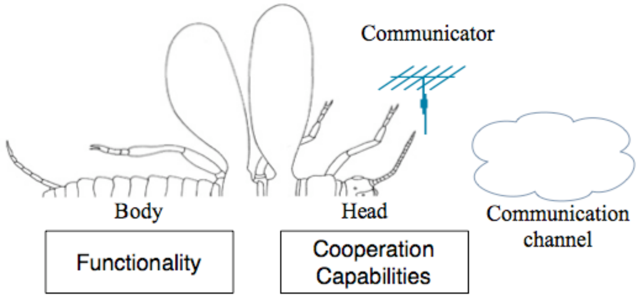

Figure 2. Insect-Inspired Generic Agent Model (Redrawn based on Borghoff and Schlichter 2000)

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