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# Inspiration from Nature: Insights from Crustacean Chemical Sensors Can Lead to Successful Design of Artificial Chemical Sensors

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## 1. Introduction

The chemical sensors possessed by crustaceans are aesthetically beautiful and are deployed in many ways, depending on the ecological task being carried out by the animal, the nature of the chemical signal, and the dispersal characteristics of the environment. As many studies have indicated, they are engineering marvels, able to detect very low concentration of odorant molecules under difficult conditions, and also able to respond to evolutionary pressures, so that over time, populations that migrate to different habitats have evolved sensor characteristics that match the features of their new surroundings.

While it may not be possible at this point to create “smart” materials that can evolve, we can learn from patterns of sensor structure observed in nature. This work typically involves comparative functional anatomy and biomechanics. We can also learn from patterns of sensor deployment. These studies examine the role of sensor movement relative to the animal, or the role of animal movement relative to the environment. These approaches often involve comparative behavioral observations of the animals followed by the development of algorithms that are then tested using biomimetic robots. The ability of the robots to perform basic olfactory tasks- such as finding an odor source- can indicate the validity of the programmed search strategies determined from animal behavior.

While interesting in their own right, these discoveries can also have profound medical, technical, and military implications. For example, researchers are investigating the use of animal-based search strategies to map chemical plumes, to pinpoint dangerous domestic gas leaks, to monitor hazardous water decontamination, to fine-tune the efforts of homeland security in detecting chemical traces, etc.

In this chapter, I plan to discuss approaches and key findings that detail the synergistic approach taken by biologists and engineers in tandem to analyze crustacean chemical sensors. I will start by describing how crustaceans use chemical sensors in a variety of impressive, ecologically critical tasks such as finding food, mates, habitat, avoiding predators, and even recognizing specific individual conspecifics. I will then detail the findings from mathematical models synthesizing these observations, as well as results from programmed robots and

autonomous underwater vehicles. Lastly, I will examine the societal benefits and outcomes of this work. I will conclude with a section on promising future directions.

## **2. Engineers and biologists work together to study biological chemical sensors**

Engineers and biologists can share their expertise about structures in order to learn how animals have evolved strategies to solve ecological problems. This knowledge can be translated to the development of technology benefiting humans or human society.

### **2.1 High performing biological chemical sensors**

Often, these projects start when biologists identify species of organisms that perform a particular physiological or ecological task at a high level. For example, male sphinx moths, after encountering a very small number of pheromone molecules, can identify and follow the odor signal released by a female moth for 1-2 miles (Ache & Young, 2005). This ability has led to significant research of insect and crustacean chemical sensors, and the strategies used by these animals to track the odors of interest to their source.

### **2.2 Fruitful team efforts**

Because of the complexity of the science, these experiments often require teams of people including organismal biologists, biomechanicians, neurophysiologists, chemists, mathematical modelers, and engineers.

### **2.3 Many techniques**

In addition to requiring a team of researchers, this work gains strength from a variety of experimental approaches. In order to properly replicate the natural environment, behavioral observations supplementing those made in the field are often made with living animals tracking odors in a carefully calibrated flume. Once the behavioral studies have been completed, the team may rely on scanning electron micrography to understand the fine structure of the chemical sensors. Because successful olfaction requires that the odor molecule come in contact with the chemical sensor, it is imperative to understand the interaction of the sensor with the surrounding fluid (air or water). Thus, a common approach is to make large, dynamically scaled models of the sensor. The resulting information can then be used in the creation of mathematical models.

## **3. Crustaceans interpret their world through chemical cues**

As humans, we are used to our perception of the world being dominated by our senses of sight and hearing. While crustaceans use those senses as well, their dominant senses are those relying on chemical sensors: smell and taste. This is especially true of crustaceans living in low light or noisy conditions.

### **3.1 Smell vs. taste**

For terrestrial animals, smell is typically used to describe the modality of detecting volatile compounds in low concentrations, while taste refers to the chemical detection that occurs

during the physical manipulation of highly concentrated material. This distinction between smell and taste is less clear in aquatic species (Ache & Young, 2005), since neither sense deals with volatile compounds in aqueous environments, and because the same compounds, or mixtures of compounds can be of interest in both senses (Caprio, 1977).

However, there may be some relevant distinctions at the chemical sensor level. All crustacean chemosensory organs for both smell and taste are chemosensory sensilla, which are small, hair-like structures containing chemosensory cells and supporting cells. These sensilla are divided into two types: bimodal chemosensory and mechanosensory sensilla located on mouthparts, walking legs, and other parts of the body, and unimodal chemosensory sensilla located on the antennules (Hallberg & Skog, 2011). The bimodal sensilla are thought to function when the chemical source is in direct contact with the animal, while the unimodal sensilla are thought to detect molecules traveling through the water. The following treatment will focus on the unimodal sensilla.

### **3.2 Roles of chemical cues in animal ecology**

Many marine crustaceans rely on water-borne chemical cues in a variety of ecologically critical activities such as finding food, mates, suitable habitat, detecting predators, and communicating with conspecifics (e.g. Atema & Voigt 1995, Caldwell 1979, 1985, Weissburg 2000, Weissburg & Zimmer-Faust 1993, 1994, Zimmer-Faust, 1989). Most crustaceans, including lobsters, crabs, crayfish, prawns, leptostracans, anaspidans, mysids, amphipods, tanaids, isopods, ostracods, phyllopods, cumaceans and stomatopods detect odors from distant sources by using unimodal chemosensory sensillae called aesthetascs (Hallberg & Skog, 2011). The following descriptions describe these activities in more detail.

#### **3.2.1 Chemical cues help crustaceans obtain food and habitat**

Environmental odors help organisms find food and suitable habitat. For example, blue crabs (Weissburg, 2000), crayfish (Moore & Grills 1999) and mantis shrimp (Mead et al., 2003) use chemical plumes to find food. At smaller spatial scales, copepods do the same (Koehl & Stricker, 1981). Spiny lobsters use chemical cues to decide whether or not to use a particular shelter (Horner et al., 2006), and anomurans are attracted by the odors emitted by large predatory snails consuming prey snails. In this case, although a food odor is the cue, the goal is not food but a potential exchange of shells negotiated at a trade “market” made up of all the attracted crabs. Even one more available shell may cause a cascade of shell exchanges (Gherardi & Tricarico, 2011). Similarly, despite the danger associated with such a signal, odors emitted by dead or damaged conspecifics are also attractive, with the goal to induce acquisition of better shells (Gherardi & Tricarico, 2011).

#### **3.2.2 Chemical cues help crustaceans find mates**

Crustaceans also use chemical substances dissolved in water to find and recognize mates. For example, male copepods can accurately and rapidly follow odor trails left by females, over hundreds of body lengths (Yen et al., 1998, Yen & Laskey, 2011). Shore crabs and blue crabs find mates and form pairs in the presence of sex pheromones (Hardege & Terschak, 2011, Kamio & Derby, 2011). Female reproductive pre-molt decapod shrimp release water soluble substances that elicit mate searching behavior in males. In some species of caridean

shrimp, large dominant males release a substance that is attractive to females (Bauer, 2011). In low density systems, the pheromone release is premolt, but in high density systems it appears to be postmolt, possibly limiting harassment (tumults) in dense populations (Bauer, 2011). Lobsters also release and detect chemical cues to find mates. Males release compounds in their urine that help female lobsters locate a potential mate. Once the females are nearby, they release chemicals that drive subsequent mating behaviors (Aggio & Derby 2011).

### 3.2.3 Chemical cues mediate social interactions in crustaceans

Once the potential partners are in proximity, pheromones mediate sexual attraction and mating readiness, but can also signal social status, aggregation, and alarm (Ache & Young, 2005). Decapod shrimp (Bauer, 2011) and anomuran crabs and lobsters (Gherardi & Tricarico, 2011) can recognize members of the opposite sex via contact chemoreception, perhaps (at least in decapod shrimp) using cuticular hydrocarbons and glycoproteins (Bauer, 2011). Chemical cues may also indicate advanced reproductive state, i.e. spawning readiness in females and sperm availability in males (Gherardi & Tricarico, 2011). Contact cues may also mediate initial pair formation in monogamous shrimp species that establish permanent bonds (Bauer, 2011).

In contrast, mantis shrimp rely on chemical cues that act over a distance to identify sex and relative social position (Mead & Caldwell, 2011). For example, mantis shrimp enter empty burrow cavities spiked with the odor of a mantis shrimp that lost a dominance battle with the test mantis shrimp much more rapidly than they enter an empty burrow cavity containing the odor of a victorious mantis shrimp (Caldwell, 1985). Dominant or subordinate status is also mediated by odors that act over a distance in crayfish (Breithaupt, 2011). During dyadic contests, crayfish emit more urine containing chemical signals as the aggression escalates, and the eventual winner emits more than the eventual loser (Breithaupt, 2011). Since urine contains the metabolites of current and recent biochemical processes, it is quite feasible that these cues contain important physiological information about the signaler. Biogenic amines such as serotonin and octopamine, implicated in aggression in crustaceans, are candidate molecules (Breithaupt, 2011).

### 3.2.4 Chemical cues are important in sibling and individual recognition

Several crustaceans employ chemical cues in sibling or individual recognition. Decapod shrimp can recognize previous pair partners, also via contact chemoreception, (Bauer, 2011). They appear to spend less time on courtship behaviors when reintroduced to previous mating partners than when encountering individuals of the opposite sex which they had never met (Johnson, 1977). A similar effect is also seen in the mantis shrimp *Pseudosquilla ciliata* (Mead & Caldwell, 2011). In other species of mantis shrimp, males are less aggressive with previous mating partners than they are with females with which they have not been paired (Caldwell, 1992). As mentioned above, mantis shrimp also recognize previous winners and losers of cavity contests (Caldwell, 1985). Lobsters (Aggio & Derby, 2011, Karavanich & Atema 1998a) and crayfish (Breithaupt, 2011) have this ability as well. Hermit crabs may have an even more refined ability to remember individuals, able to identify a conspecific as familiar outside the winner/loser dichotomy (Gherardi & Tricarico, 2011). This recognition appears to be associated with properties of the shell.

### **3.2.5 Chemical cues assist in avoiding predators**

Chemical cues are not necessarily attractive; in the case of predator cues or of damaged conspecifics, they are usually repulsive. For instance, blue crabs avoid traps baited with injured conspecifics (Hay, 2011). Crustaceans can exhibit a variety of responses to chemical cues (crushed conspecifics, or predator odor), such as decreasing their forward movement, reducing movement in any direction and assuming protective positions, moving away from the source of odor, increasing defensive displays, and increasing preference for protective habitats (Hazlett, 2011). When crayfish are exposed to a combination of food odors and predator odors, they reduce their foraging, increase their use of refuges, and avoid the alarm odor by spending more time outside of the odor plume (Tomba et al., 2001). Of course, this results in a decrease in foraging success.

## **4. Crustacean chemosensor structure**

All chemosensory sensilla contain ciliated bipolar sensory cells. The bimodal sensory cells, are thought to function in contact chemosensation. In contrast, most of the cues described above that act over a distance are detected by unimodal chemical sensors called aesthetascs. The description below focuses on aesthetascs. In order for distance chemoreception mediated by aesthetascs to work, the odor molecules must first be transported to the surface of the aesthetasc, the cuticle. The morphology of the aesthetascs, their arrangement on the antennule, and the movement of the antennule relative to ambient water motion affect the flow of water bearing odorants around the sensillae. This in turn affects the transport of odorants to the aesthetasc surface and hence to the chemoreceptors within the sensillae. Thus, the structure and deployment of the antennules affect the ability of the animal to identify the contents of the plume and locate its source

### **4.1 Contact chemoreception is usually mediated by bimodal sensilla**

Bimodal sensilla contain both chemosensory and mechanosensory cells. These structures typically have a thick, dense cuticle with an apical pore, and are arranged all over the body but especially densely on the mouthparts and walking legs (Hallberg & Skog 2011). They can be large and robust, as in the lobster hedgehog sensilla, or small and slender, as in some crab bimodal sensilla. Often the former are found on the walking legs while the latter are found on mouthparts, antennae, and antennules (Hallberg & Skog 2011).

### **4.2 Chemoreception of odor from distant sources is usually mediated by aesthetascs and antennules**

The most common unimodal sensillum found in crustaceans is the aesthetasc. Aesthetascs are stiff, cuticular hair-like structures organized in arrays found exclusively on the antennules (Hallberg et al., 1992). Aesthetascs are typically long and slender, varying from 5-30  $\mu\text{m}$  in diameter and 10-1400  $\mu\text{m}$  long, depending on the species and the age, sex, and condition of the individual, and the flow habitat. For example, aesthetascs in low flow environments tend to be longer and more sparsely arrayed, to facilitate odorant access (Ziemba et al., 2003, Mead, 2008). In contrast to bimodal sensilla, aesthetascs have a porous cuticle that allows low molecular weight molecules to pass through, thus acting like a molecular sieve (Gleeson et al., 1993). Male-specific sensilla, another type of unimodal olfactory sensilla, are found in only a few groups, including mysids (Hallberg & Skog, 2011).

### 4.3 Two signaling pathways

The dichotomy of the two types of chemoreceptors is reflected in the organization of the CNS pathways. Evidence from spiny lobsters and other crustaceans suggests that many crustaceans possess two pathways that contribute to chemically mediated responses (Mellon, 2007, Schmidt & Ache, 1996, Schmidt *et al.*, 1992). In the olfactory pathway, olfactory neurons within the aesthetascs project into a synaptic region of the midbrain called the olfactory lobe which is organized in dense regions called glomeruli (Schmidt & Ache, 1992). The non-olfactory chemoreceptive pathway involving contact chemoreception via bimodal sensilla projects onto a variety of synaptic areas distributed throughout the brain and ventral nerve cord (Schmidt & Mellon 2011).

### 4.4 Aesthetasc cellular structure and receptors

Within the cuticle, each aesthetasc typically has between a few to a hundred bipolar sensory cells, which may have highly branched outer dendritic surfaces. This multiplicity of neuronal processes is thought to increase the surface area for stimulus capture. (Ache & Young, 2005). The outer dendritic surfaces are sprinkled with odor receptors, which are G protein coupled receptors (Buck & Axel, 1991). It is thought that each sensory bipolar neuron expresses one receptor type, and projects to one glomerulus.

### 4.5 Variable number of sensors in the array

The number of aesthetascs per antennules is variable. Burrowing decapods such as *Upogebia* spp. and *Callinassa* spp. have 15-22 aesthetascs per antennules (Hallberg & Skog, 2011). Decapods such as *Panulirus argus* have between 1,200 and 2,400 aesthetascs, depending on the size of the individual (Hallberg & Skog, 2011). It is not yet known to what extent this difference in sensor number is reflected in olfactory use or ability to use olfaction in the various tasks outlined in section 3.

#### 4.5.1 Role of number of sensors

Especially when considering how knowledge of animal sensors can be applied to artificial sensors, it can be interesting to speculate on the performance advantage conferred by multiple sensors (Derby & Steullet, 2001). This question can be considered biologically, chemically, and physically. In terms of biology, crustaceans rely on olfaction for a number of critically important ecological tasks, sometimes involving exquisitely complicated behavior. It stands to reason that there would be a many-sensored apparatus capable of resolving nuanced information to support these tasks. Also, given the developmental or molt stages in which aesthetascs are nonfunctional and also the inevitable damage likely to sensor arrays belonging to crustaceans that engage in aggressive encounters, it would be practical to have some redundancy. Chemically, more sensors might mean that more odor molecules, or more mixtures of compounds, are distinguishable. Similarly, many sensors allows for the possibility of range fractionation. If different populations of sensors sensitive to the same molecule are responsive at different concentrations, more sensitive measurements and responses might be possible. In terms of physics, range fractionation could also occur in terms of temporal dynamics. As a result, different populations of sensors responsive to the same molecule might respond and thus adapt over different time courses, resulting in

subsets of receptors best able to detect slow, medium, or rapid changes in chemical concentrations. This ability could also be important in some models of odor plume navigation. As we will see later, the arrangement of sensor arrays is important too. Some of the methods of following odor plumes to their source require at least two sensor arrays, for spatial comparison of odor concentration. Lastly, larger arrays, with more sensors, have an increased probability of encountering chemical signal. This increase in size could be especially important in flow conditions that give rise to sparse odor filaments within the odor plume envelope, as described below.

#### 4.5.2 Role of shape of sensor

Crimaldi et al. (2002) used physical and mathematical models to analyze the effect of sensor size and shape, among other characteristics. When they used similar-sized sensors that were either square-shaped or long, skinny rectangles, they found that the linear arrangement was much more efficient at capturing odor signals from the environment when the average odor concentration was low, but that the square arrangement had better performance when the average odor concentration was high.

#### 4.5.3 Sensor response time

The odor-containing filaments within the odor plume are often very narrow, and thus of short duration. Therefore, chemical sensors with a slow response time (e.g. slower than 100 Hz, for a small sensor) are apt to register lower concentrations than the actual peak concentration encountered because the peak is temporally “smeared” over the entire response time of the sensor. Thus, the likelihood of detecting large concentrations decreases dramatically as the temporal response of the sensor becomes slow (Crimaldi et al., 2002). Interestingly, large sensors are less sensitive to this temporal smearing, with a cut-off of about 10 Hz rather than the 100 Hz for the small sensors. Smearing also occurs spatially. Because odor filaments are highly localized, large sensors operating at a low frequency (e.g. slower than 1 Hz) are apt to register lower concentrations than the actual peak signal encountered because the signal is averaged over the full extent of the sensor and effectively diluted.

### 5. Odor plume structure

The dispersal of chemical signals is controlled by the physics governing flow. At low flow velocities and at small length scales, flow is dominated by viscous processes. In this laminar regime, experienced by animals such as copepods, streamlines do not cross, and the odor plume is relatively coherent (Weissburg, 2011). Animals attempting to follow such an odor plume would experience sharp gradients in chemical concentration, especially in the cross-stream direction. In contrast, many animals, especially those in coastal and/or wavy environments, experience more turbulent flow regimes. These environments are characterized by unpredictable velocity fluctuations, leading to fluctuations in the chemical concentrations of odor plumes downstream from the odor source. In these circumstances, experienced by many larger benthic crustaceans including crabs, lobsters, crayfish, and mantis shrimp, turbulent odor plumes are composed of filaments of odor-laden water interspersed with odor-free fluid (e.g. Crimaldi et al., 2002, Crimaldi & Koseff, 2001, Koehl, 2006, Moore & Crimaldi 2004, Moore et al., 1991, Moore et al., 1994, Webster et al., 2001,



Weissburg, 2000). The structure of an odor plume (and thus how the plume is encountered by navigating animals) is affected by several flow and substrate characteristics including the mean velocity, the turbulent intensity, the presence of waves and the gradient of flow speed above the substratum (the current boundary layer) (Crimaldi & Koseff 2001). As flow becomes more turbulent, the odor filaments typically thin, elongate, and have lower odorant concentration. This is probably because the more numerous eddies stretch the odor-containing fluid into longer elements that increase the surface area across which diffusion can act. Often the odor filaments are more numerous (Finelli, 2000), and more often above a concentration threshold (Crimaldi & Koseff 2001). Different substrates, such as sand, gravel or cobble, and the type of vegetation growing on the substrate, give rise to different boundary layer features and different chemical signal structures due to changes in the turbulent intensity (Finelli, 2000, Moore et al., 2000).

### **5.1 Effects of plume structure on plume tracking**

These differences in hydrodynamics affect plume tracking success. Blue crabs are more successful at finding odor sources when the flow speed is above 1 cm/s, and walk straighter and more directly upstream as flow velocity increases (Weissburg & Zimmer-Faust, 1993, Finelli et al., 2000). Stomatopods are more successful at finding odor sources in wave-affected flow than in unidirectional flow (Mead et al., 2003). Crabs find odor sources more efficiently on a cobble substrate rather than on sand (Moore & Grills, 1999).

### **5.2 Features of odor plume structure of interest to navigating crustaceans**

It is not clear precisely what aspects of environmental odor signals are important to the animal, but progress has been made in terms of understanding the responses of olfactory neurons. Different olfactory cells probably respond to different aspects of odor filament structure, but at least some olfactory neurons appear to be sensitive to peak odor concentration and odor pulse duration (Gomez & Atema, 1996a, 1996b; Gomez et al., 1999). In addition, models and experiments suggest that sensory cells can distinguish between different rates of increasing odor concentration (onset slope) (Kaissling, 1998a, 1998b, Rospars et al., 2000, Zettler & Atema, 1999).

## **6. How crustaceans deploy their sensors**

Many crustaceans create some kind of movement or current to facilitate olfaction. In some cases, the movement is by the signaler, as in the case of chemicals emitted in urine streams directed forward by strong gill currents in crayfish (Breithaupt, 2011). Since urinary distribution of chemical cues, especially sex pheromones, and gill currents, are common in crabs and lobsters (Aggio & Derby, 2011), it is probable that these odor-laden streams or jets are common among the decapod crustaceans. These jets can impart significant energy to the surrounding flow (Weissburg 2011). Pleopod fanning, used by crayfish (Breithaupt, 2001), male blue crabs (Weissburg, 2011) and mantis shrimp (Mead & Caldwell, 2011), and maxilliped pulsing, used by mantis shrimp (Mead & Caldwell, 2011) are other movements used to increase the transport of scent away from the animal.

Animal movements can facilitate chemoreception as well. Pleopod fanning and maxilliped pulsing can be used by mantis shrimp to create currents that draw water past chemosensory

surfaces (Mead & Caldwell, 2011). Crayfish use a fan organ for the same task (Breithaupt, 2001).

Other movements or currents are generated only by the receiver. For example, many crustaceans move their antennules- and thus their aesthetascs- through the surrounding medium to facilitate odor reception. One common movement found in crayfish, lobsters, crabs, mantis shrimp, and other crustaceans is an olfactory flick (Koehl, 2011). Other receptive sensor movements include antennulation in mantis shrimp (Mead & Caldwell, 2011). These currents or movements of the sensory appendages allow chemical cues to better penetrate the sensory arrays. The sensor movements implicated in signal reception and the ways in which the motions benefit olfaction are further described below.

### 6.1 Pleopod fanning and other fan organs

Pleopod fanning or use of crayfish fan organs can create large, local currents greater than the ambient flow. When crayfish fan organs are restrained so that no current is produced, they are unable to localize odor sources (Breithaupt, 2001). Recent field observations of *Squilla empusa* (Mead, unpublished) indicate that mantis shrimp often lurk at the entrance of their burrows with their eyes and antennules near the substrate surface. In this orientation, pleopod fanning draws fluid into the burrow past the antennules. Mantis shrimp appear to engage in pleopod fanning when a variety of olfactory stimuli- food odors, predator odors, odors from conspecifics- are presented. Since these mantis shrimp currents are also essential for keeping oxygenated water moving through the burrow, it has not been possible to test the effect of pleopod fanning currents on olfactory response by restraining the pleopods, because this would quickly be lethal. However, since the benthic boundary layer near the mantis shrimp burrows is typically on the order of 2-3 cm, it is likely that mantis shrimp lurking in burrows would be less likely to detect, let alone respond to, olfactory stimuli in the absence of pleopod fanning.

### 6.2 Maxilliped pulsing

Maxilliped pulsing creates more local and more transient changes in water flow and thus in chemical signal distribution. Maxilliped pulsing is often seen in burrow occupants as an intruder is approaching the entrance. The movement consists of a series of simultaneous anterior extensions of multiple pairs of maxillipeds toward the intruder. The appendages move in circular strokes, with cycle rate, extension distance, and the openness of the maxilliped dactyls all increased the closer the male came to the entrance. Although dye studies indicate that most of the resultant fluid motion is away from the occupant, small return currents bring water from the side and across the female's antennules (Caldwell 1992). Maxilliped pulses, therefore, may function to both send and to receive signals.

### 6.3 Antennulation

Antennulation consists of the forward extension of the paired antennules coupled with short, quick oscillations in the vertical plane (Caldwell, 1992). Antennulation typically occurs as a male is approaching a cavity inhabited by a female, possibly to garner information about the inhabitant's reproductive status and to determine, if female, if the occupant is a previous mate. Antennulation appears to be a subcategory of olfactory flicking

used by mantis shrimp in many investigatory situations, such as in response to a food odor or in tracking an odor to its source.

#### **6.4 Olfactory flicking**

Olfactory flicking describes an antennule odor sampling movement observed in many crustaceans. In all crustaceans studied to date, including shrimp, mantis shrimp, crabs, crayfish, and lobsters (Koehl, 2011), each flick has two parts: a rapid, outward lateral movement followed by a slower return medial movement. The functional importance of flicking, and indeed of all the other sensor movements described in this section, is based on the idea of a boundary layer.

#### **6.5 A layer of slow-moving fluid coats the antennules**

An antennule immersed in a fluid can be roughly thought of as having layers of fluid coating every surface. Because of the “no-slip” condition, the layer of fluid closest to the antennule’s surface does not move with respect to that surface. Thus, a velocity gradient forms in the fluid between the antennule and the mainstream flow. Typically, the distance from the surface to the point where the velocity is 99% of the mainstream velocity is called the boundary layer (e.g., Vogel, 1994).

#### **6.6 Olfactory sampling currents and movements “thin” the boundary layer, speed up the delivery of chemical cues, allow discrete sampling, and increase the probability of signal encounter**

When the appendage moves rapidly through the fluid (in a flick or an antennulation), or when the ambient flow is fast relative to the antennule (because of environmental flows or animal-created currents such as pleopod fanning), the boundary layer of slow-moving fluid coating the antennules gets thinner. The thickness of the boundary layer is very important for olfaction because it can act as a barrier to odorant access to the aesthetascs. While odorants can be very rapidly transported through the environment in currents (at speeds on the order of centimeters to meters per second), the time required to cross the boundary layer relies on the much slower process of molecular diffusion.

Thus, flicking can speed up the delivery of chemical cues to the surface of the aesthetasc. Advection-diffusion models using data from dynamically scaled physical models of mantis shrimp antennules indicate that odor molecules in filaments moving into the sensor array arrive at the surfaces of the aesthetascs within milliseconds (Stacey et al., 2003). In contrast, during the slower return stroke of the flick and during the stationary pause between flicks, the just-sampled fluid remains in a layer coating the sensors, and new, odor-containing fluid flows around rather than into the array of chemosensory hairs (Mead et al., 1999; Mead & Koehl, 2000). Thus, an antennule of a mantis shrimp takes a discrete sample in time and space of its odor environment only during the flick outstroke (Mead & Koehl, 2000, Stacey, et al., 2003). This pattern of discrete sampling appears to be widespread among crustaceans (Koehl, 2011). Other ventilatory mechanisms in other phyla have similar functions, suggesting that the ability to take discrete samples of the chemical environment is integral to the success of odor discrimination (Ache & Young, 2005). Lastly, physical and mathematical modeling of lobster flicks indicate that flicking increases the likelihood that the antennule encounters peak concentrations of signal (Crimaldi et al., 2002).

## **6.7 The frequency of sensor movements**

When a crustacean samples water with a flick outstroke, the movement of the antennule changes the rate at which chemical signals are encountered. If the flicking is against the mainstream flow, (i.e. the animal is angled upstream) the velocity of the antennules relative to the ambient flow will be increased, so that the speed of signal encounter will increase. In addition, since flicking into the direction of flow also increases the area of the plume that is sampled, flicking antennules encounter more odor relative to stationary antennules (Crimaldi et al., 2002).

## **7. Crustaceans are able to localize odor sources**

Once crustaceans have detected chemical cues from distant sources, identified them, and determined that they are of interest, they often have to navigate the odor plume to its source to find food, habitat, or a mate. The difficulty of this task depends both on the flow environment, which sculpts the odor signal, and on the sensory and locomotory abilities of the animal. Organisms tracking odors must sample the odor signal, usually by moving their chemosensitive organs through the odor-containing medium, or by creating currents that bring the odor to the chemosensors. Since odor plumes consist of fine filaments of concentrated odor molecules interspersed with the surrounding fluid, and since the filaments can be twisted along all axes and the entire plume can meander, the organism has to continuously sample the plume to get updated information about possible locations of the source. This can lead to more complicated tracking strategies than those found in organisms orienting to light or sound. Various taxes and odor localization schemes have been proposed to describe these odor plume search strategies.

### **7.1 Navigating using presence/absence of odor and flow direction**

One of the simplest navigational strategies proposed is odor-gated rheotaxis. In this strategy, an organism moves upstream as long as it detects odor above a threshold concentration or frequency. This strategy requires only the ability to distinguish between absence and presence, and the ability to determine the direction of flow. Behavioral data sets in support of this idea include the fact that some crustaceans do not respond to odor cues in the absence of flow (Weissburg & Zimmer-Faust, 1993).

### **7.2 Navigating using time-averaging and temporal comparisons**

An organism searching odor sources using klinotaxis moves upstream as long as sequential measurements show a stable or increasing concentration of odor. For this to work, each measurement has to reflect a time-averaged signal, since instantaneous measurements of odor concentration fluctuate over orders of magnitude. Most crustaceans do not appear to sample long enough or fast enough in one location to be able to reliably estimate average odor concentrations. This strategy has been hypothesized to be most effective in large, slowly moving predators such as starfish, whelks, and catfish.

### **7.3 Navigating using spatial comparisons**

Many crustaceans appear to be using a variation of strategies in which the organism compares inputs to more than one chemosensory structure, for example left and right

antennules. Removing the chemosensory structures on one or both sides limits plume-tracking success in crayfish (Kraus-Epley & Moore, 2002). In the version of the spatial comparison strategy used by lobsters, the animal appears to turn slightly to the sensor that intercepted the highest chemical concentration. The lobster thus remains in the “center” of the odor plume, where there is a greater likelihood of encountering concentrated odor filaments (Weissburg, 2011). Other navigational strategies relying on spatial comparisons seem to cause animals to move upstream when the left and right chemosensory inputs are different. This mechanism could result in animals tracking the “edges” of plumes, as blue crabs (Weissburg, 2011) and mantis shrimp (Mead et al., 2003) appear to do, because the antennules closest to the plume “center” would have a greater likelihood of encountering high concentration than the antennules sampling in a more lateral position. Note that plume “center” and plume “edge” are statistical concepts only evident after long time-averaging.

#### **7.4 Other navigational strategies used by very small crustaceans**

While probably all organisms can detect some classes of chemicals, organisms that are very small may have difficulty detecting the differences in concentration across space that could assist in orienting to an odor source. It is possible that some very small crustaceans, like bacteria, adopt a kinesis strategy in which they move in larger randomly oriented steps when subject to low concentration, and smaller steps when exposed to high concentration. Eventually, this ‘random walk’ positions them in areas of higher concentration. Other microorganisms alter their rate of rotation, with similar effect (Vogel, 1994).

### **8. What can we learn from animal sensors to apply to artificial sensors?**

Table 1 sums up some of the factors affecting performance in crustacean chemical sensors discussed in sections 4-7. The summary is broken into 1) structural factors affecting the isolated sensor, flow factors affecting chemosensor performance, and animal factors affecting sensor performance.

#### **8.1 Design principles**

Studies of crustacean chemosensor design suggest that artificial chemical sensors should be composed of multiple small elements, distributed spatially across the platform. The sensors should be as sensitive as possible, and sample at a high frequency, in order to detect the maximum number of encountered odor filaments. The ability to make simultaneous spatial comparisons between at least two sensors facilitates plume tracking (Webster et al., 2001).

#### **8.2 Role of movement**

Artificial sensors will probably be the most effective if they can move through the environment or have the fluid medium flow past them. A repetitive, asymmetrical movement analogous to the ubiquitous crustacean flick will 1) hasten the arrival of the chemicals at the sensor array, 2) facilitate the creation of discrete samples, and 3) increase the size of the sample space.

Factor	Effect	Rationale
<b>Factors affecting sensor performance</b>		
Number of sensors	More sensors better	Redundancy, can detect more chemicals, accuracy, range fractionation, if can compare between arrays can probably navigate to source more effectively
Size of sensor array	Bigger array better	Can intercept more signals; many small sensors better than one big one, to avoid spatial smearing
Ability to resolve discrete samples	Essential	Can potentially make temporal comparisons, necessary for some navigational schemes
Sample frequency	Higher frequency	Higher frequency leads to less temporal smearing, so more odor filaments encountered
<b>Factors affecting flow and/or odor plume structure</b>		
Ambient current	Can be essential	Current aids in establishing directionality
Current or sensor movement produced by animal	Aids in signal reception	Can improve chemical cue reception by favoring advective transport over slow molecular diffusion, but will affect signal downstream
Turbulent mixing	Can increase or decrease navigation success	Turbulent mixing increases plume volume, increasing the likelihood that animals will encounter signal, but decreasing signal strength via mixing
Substrate roughness	Can increase or decrease navigation success	Turbulence increases as substrate roughness increases; this can positively or negatively affect a sensor's ability to detect signal
<b>Factors affecting odor plume navigation</b>		
Animal size	Large animals have better spatial sampling	Bigger animals can use spatially distributed sensors
Animal mobility	More search strategies available to slow animals	Slow animals may be able to employ time-averaging
Animal antennules flicking	Facilitates plume tracking	Increases encounter of peak concentration

Table 1. Factors affecting crustacean chemical sensor performance

### 8.3 Applications in medical, technical and military realms

There are many potential applications of knowledge about crustacean chemosensors to the medical, technical, and military fields. Recently, several groups have developed autonomous, chemical sensing robots that can track odors using strategies derived (in part) from crustaceans (Grasso, 2001, Ishida et al., 2001). Large scale devices could work in open

environments to find and destroy unexploded mines or repair leaks of toxic substances. Small scale devices could potentially detect and identify odors of life-threatening chemicals in enclosed hospital environments, or even within the human body. Other applications include quality control in industrial settings. Most of these developments have been based on developing sensors appropriate for the task at hand, and combining them with the tactic strategies employed by living organisms.

### **8.3.1 Human health applications**

Pathfinding using chemical cues is an important process with many applications in normal growth and development. For instance, the location of certain chemoattractants in the extracellular matrix (ECM) can be critical for the appropriate laying down of new neurons (neurogenesis) and blood vessels (angiogenesis). The subversion of these processes is implicated in some forms of cancer metastasis, and in many other diseases and syndromes, including atherosclerosis, arthritis, infertility, and tooth decay. If we better understand sensors and odor trail navigation, we might be more equipped to predict and treat malfunctions of chemical sensor operation in the body. Furthermore, the body emits characteristic odors via the skin, blood, urine, and breath. These odors reflect genetics, physiological state, diet, metabolic condition, age, the immune response, and the effects of stress by virtue of VOCs (volatile organic compounds). Typically, there is no one particular marker of state or disease, but changes in the relative abundances of key VOC components. For example, VOC changes due to schizophrenia can be detected in skin odor, alterations in blood VOCs may indicate liver cancer, breath VOCs may predict diabetes, breast cancer, and cystic fibrosis, and urine VOCs may help diagnose urinary tract infections (Oh, et al., 2011). It has been possible to study at least some of these VOCs using gas chromatography, mass spectrophotometry and other methods, but these techniques have been time-consuming and expensive. Electronic noses are small, portable, cheaper to use once developed, and give results more quickly.

#### **8.3.1.1 Structure of electronic and bioelectrical noses for biomedical applications**

Currently, there are research and commercially available electronic noses based on a variety of nanotechnologies including metal oxide semiconductor sensors, conducting polymer-based sensors, piezoelectric sensors, and optical sensors, described beautifully in Oh, et al. (2011). A new generation of bioelectrical sensors is also being developed. These bioelectrical noses consist of harvested or cultured cells or odorant receptors grown or otherwise attached to microchips that respond with an electrical output as part of the odor signal transduction process. Both the electronic noses and bioelectrical noses represent areas of active research. Two of the most promising health applications using electrical noses will be described below.

#### **8.3.1.2 The detection of bacterial populations**

Dutta et al. have used an electronic nose consisting of 32 black carbon composite conducting polymer sensors to distinguish between populations of bacteria (2002). When VOCs are introduced to the system, any of the 32 individual sensors that bind to any of the VOCs swell and change their conductivity. These changes create a combinatorial profile in the 32 sensors that can be analyzed via principle component analysis to identify specific species and types of bacteria. One of the most interesting (of many!) applications of this sensor has

been to detect and distinguish MRSA (methicillin resistant *Staphylococcus aureus*) and MSSA (methicillin susceptible *S. aureus*; Dutta et al., 2005). In this report, swabs from infected areas of patients were placed in 15 ml vials for 5 minutes, to allow the aromatic compounds to volatilize. The resulting sample was then “sniffed” by the electronic nose. Using innovative data clustering techniques, Dutta et al. (2005) were able to identify bacterial classes with very high accuracy. If placed in hospital ventilation systems, this electronic nose could theoretically detect and prevent contamination of other patients or equipment.

### 8.3.1.3 The use of electronic noses to detect lung cancer

Peng et al. (2009) have developed an electronic nose based on cross-reactive chemiresistors in which the organic molecules that respond to particular odorants are adsorbed onto gold nanoparticles. The gold/organic film lies between adjacent electrodes; the resistance between the electrodes changes in response to odorant binding, which probably causes the film to swell. The sensors were able to distinguish between breath samples from healthy and cancerous individuals with > 86% accuracy and >90% repeatability.

## 8.3.2 Industrial and military use

Artificial noses are also used to monitor VOCs in industrial settings. Recent uses include monitoring the quality of tea (Dutta et al., 2003), and checking pork products for the presence of boar taint (Wäcker et al., 2010). The electronic noses used by Dutta and others are typically used in a stationary manner, with the sampled air drawn into the apparatus much like a vertebrate sniff. Other artificial chemical sensors are being developed for robotic platforms, so that they could not only identify chemical compounds, but search and find them, much as insects and crustaceans follow odor plumes in the environment.

### 8.3.2.1 Autonomous electronic nose searching platforms

In addition to the high sensitivity, selectivity, and rapidity of response that are optimal in all electronic noses, autonomous sensors expected to move freely in an environment must also be small, consume power efficiently, and be robust enough to withstand the elements and any other hazards. Common approaches for these sensors include tin oxide sensors and quartz microbalance sensors (Russell, 2001). Tin oxide sensors work on the principle that when the heated sensor encounters reducing gases, resistance decreases. Quartz crystal microbalances function by detecting changes in crystal resonant frequency as the chemical of interest is adsorbed onto the quartz. Robotic platforms equipped with at least two of these sensors and an inward drawing fan to facilitate odor interception have been programmed with variations on the plume searching and plume tracking algorithms used by crustaceans described in section 7.3. (Kowadlo and Russell, 2008). These robots were 70%-100% successful, depending on the nature of the flow field, the odor source, the particular robot platform, and the signal processing algorithm.

Encouraged by the success of trained dogs at finding explosives, researchers are excited about the possibility of developing odor-searching robots that could find traces of TNT and other explosives. These robots could potentially find and signal the presence of unexploded ordinance, old abandoned mines, and other hazards (Russell, 2001). Other potential uses include implants or roving sensors that could warn of the presence of natural gas, radioactive material, or could monitor water quality, especially during the clean-up of



hazardous materials. In addition to the unexploded ordinance application mentioned above, field-deployed sensors could also help to detect the presence of biological toxins and other agents of war. These latter applications would have the advantage of limiting human exposure to potentially lethal situations. In an interesting, iterative relationship, one of the most potent applications of the artificial sensors coupled with robotic, motile platforms is to test the search algorithms predicted from animal behavior. This approach has been used effectively by Grasso (2001), Ishida (2001), and others.

## 9. Future directions

While much progress has been made, much work remains to be done, in terms of both basic science and its applications.

### 9.1 Basic science

From a basic research perspective, the chemicals used in olfactory signaling are still unknown, in all but a few cases. Furthermore, it is suspected that in most cases, the cues consist of mixtures of compounds. The ways in which nuanced physiological condition could be communicated via small alterations in ratios of mixtures will no doubt be a fruitful area of future study. Another important future topic for both basic and applied scientists should be the role of the multiple sensory modalities used simultaneously by many crustaceans and available for sensor designers. For instance, mantis shrimp probably use vision as well as their sense of smell, at least when light conditions are favorable, and copepods and crabs rely on hydromechanical cues as well as olfactory signals.

Other basic questions involve the role of deception using chemical signals, the energetic costs to chemical signaling, and the social costs of chemical signaling. These questions are connected. For instance, when is it against an organism's interest for information about its physiological state to be broadcast into the environment?

### 9.2 Applied aspects

While the chemical sensors deployed in a industrial or hospital setting may face predictable environments, one of the biggest challenges to using chemical sensors in the field is the unpredictability of the flow environment. Many features of the odor plume- peak odor concentrations, filament width, filament sharpness, etc. vary both with environmental factors and with distance from the source. Different odor plume tracking strategies used by crustaceans may work best under different flow conditions, and some crustaceans even seem to vary their strategy based on odor plume structure (Grasso, 2001). Thus, it will be important to develop autonomous devices that can flexibly and intelligently adopt the best navigational strategy given the task, the habitat and the available odor signal, even more so than as described in Kowadlo and Russell (2008). Lastly, the ability to deploy different sensors given the exigencies of the environment would be an asset. Here, too, the use of multiple sensory modalities should be a future topic (Grasso, 2001, Grasso & Atema, 2002).

## 10. Conclusions

In conclusion, crustacean chemical sensors are remarkably effective structures that are essential in helping these animals complete a variety of critical ecological tasks. By studying

crustacean chemical sensors, we can both contribute to the understanding of important biological questions and provide inspiration to engineers trying to create artificial sensors that can carry out important and dangerous tasks for humans.

## 11. Acknowledgements

I am grateful to InTech for the invitation to submit this chapter, to Denison University for funding during part of the writing period of this chapter, to the Marine Biological Laboratory for access to their wonderful library holdings, and to Breithaupt and Thiel's book *Chemical communication in crustaceans*, a great resource.

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## **Advances in Chemical Sensors**

Edited by Prof. Wen Wang

ISBN 978-953-307-792-5

Hard cover, 358 pages

**Publisher** InTech

**Published online** 20, January, 2012

**Published in print edition** January, 2012

The chemical sensor plays an essential role in the fields of environmental conservation and monitoring, disaster and disease prevention, and industrial analysis. A typical chemical sensor is a device that transforms chemical information in a selective and reversible way, ranging from the concentration of a specific sample component to total composition analysis, into an analytically useful signal. Much research work has been performed to achieve a chemical sensor with such excellent qualities as quick response, low cost, small size, superior sensitivity, good reversibility and selectivity, and excellent detection limit. This book introduces the latest advances on chemical sensors. It consists of 15 chapters composed by the researchers active in the field of chemical sensors, and is divided into 5 sections according to the classification following the principles of signal transducer. This collection of up-to-date information and the latest research progress on chemical sensor will provide valuable references and learning materials for all those working in the field of chemical sensors.

### **How to reference**

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Kristina S. Mead (2012). Inspiration from Nature: Insights from Crustacean Chemical Sensors Can Lead to Successful Design of Artificial Chemical Sensors, *Advances in Chemical Sensors*, Prof. Wen Wang (Ed.), ISBN: 978-953-307-792-5, InTech, Available from: <http://www.intechopen.com/books/advances-in-chemical-sensors/inspiration-from-nature-insights-from-crustacean-chemical-sensors-can-lead-to-successful-design-of-a>

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