From taste to touch: sensory signaling in model organisms

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The ability to perceive our environment has fascinated scientists and philosophers for thousands of years. According to some interpretations of Aristotle's writings, the sense organs are able to perceive the environment by being transformed so that they are more like the object they are detecting. An eye can see a specific color by taking on that color; an animal can perceive warmth by becoming warm, and so forth.

In recent years, our understanding of the inner workings of the Aristotelian senses of sight, smell, taste, touch, and hearing has gone through a revolution, and many of the key insights have emerged through analyses of model organisms. The reviews in this special issue of Pflügers Archiv highlight the progress achieved through work in genetically tractable metazoan animals ranging from worms to flies and mice. Although the various sensory modalities operate through a diversity of activation mechanisms and time-scales, a recurring theme is that members of the transient receptor potential (TRP) superfamily of cation channels function broadly in sensory physiology and throughout animal phylogeny.

The most ancient among the five classical senses are touch, taste, and smell. These three sensory modalities are present in the worm, *Caenorhabditis elegans*, and all metazoan organisms analyzed. In fact, the first mutations to affect touch were identified in the worm, and a review by Alexander Bounoutas and Martin Chalfie describes the current state of knowledge of the cells and proteins that function in the response to gentle touch. The fruitfly,

Drosophila melanogaster, has also been invaluable for dissecting the genetics of gentle and noxious touch, and Maurice Kernan reviews the functions and development of the various types of sense organs in flies and the proteins essential for mechanotransduction. Among the players identified is no mechanoreceptor potential C (NOMPC), which is required for light touch and is the first TRP channel shown to function in mechanotransduction.

The other of the primordial sensory modalities, taste and smell are important not only for identifying nutrient-rich sources but for avoiding noxious chemicals and predators. In many animals, the pheromone response contributes to mate selection, mating behavior, aggressiveness, and other behaviors. In worms, chemosensation impacts on a developmental program as the animals arrest at a nonreproductive, nonfeeding stage in environments with a paucity of food or food-derived odors. The perception of chemical cues in the environment can also impact lifespan, at least in invertebrates.

Four reviews in the current special issue focus on the responses to volatile (olfactory) and nonvolatile (gustatory) chemical stimuli. These include a contribution by Piali Sengupta, outlining the cells, circuitry, and molecules involved in chemically induced behaviors in worms. Michelle Ebbs and Hubert Amrien provide an overview of the anatomical sites and receptors required for the taste and pheromone responses in *Drosophila*. In addition, they review fly taste transduction and the behaviors controlled by nonvolatile chemicals. As outlined in a separate review by Dean Smith, *Drosophila* has also provided important insights into the detection and processing of olfactory stimuli. While most pheromones are nonvolatile, at least one volatile chemical serves as a pheromone in flies, and this latter review describes the requirement for this pheromone for mating and for aggressive behavior.

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Among the seminal findings in mammalian chemosensation are the discoveries of large families of olfactory and taste receptors and the molecules involved in transducing the signals. Steve Roper reviews the mechanisms underlying the reception of sour, salt, sweet, bitter, and umami stimuli and the downstream signaling events. In addition, Roper discusses how the tastant-induced signals are processed within the taste buds and ultimately carried to the central nervous system.

The capacity to sense variation in environmental temperatures is also a primitive adaptation and is crucial for animal survival. Detection of thermal input allows animals not only to avoid detrimental temperatures but, along with other sensory inputs, contributes to the identification of prey and predators. David McKemy reviews the remarkable recent progress defining the cells and molecules functioning in thermosensation in worms, flies, and mammals. Not least among the discoveries are the reports that members of the TRP superfamily are essential thermosensors in flies and mammals. A common feature of mammalian thermoTRPs is that they also activated directly by botanical compounds. This property provides a molecular explanation for the long-known observation that certain compounds, such as menthol and capsaicin, elicit the same sensations as thermal cool and heat.

In the more complex metazoan organisms, mechanotransduction also facilitates the detection of acoustic stimuli. In addition to the obvious functions for hearing, flies use sound detection for mating, as males vibrate their wings to produce an acoustic stimulus (courtship song), which stimulates receptivity in the female. The review by Maurice Kernan mentioned above also includes a synopsis of the mechanics and molecules involved in auditory transduction. Lisa Grant and Paul Fuchs discuss exciting progress in the area of auditory transduction in mammals, which has been achieved in part through genetic, electrophysiological, and biochemical analyses in the mouse. In mammals, the detection of acoustic stimuli takes place in hair cells of the cochlea, which contain a bundle of stereocilia. Sound-induced deflection of the bundle leads to activation of the auditory transduction channels and cation influx. Although the transduction channel remains enigmatic, mutations in two mouse TRP channels cause hearing loss phenotypes. In addition, Grant and Fuchs describe the considerable progress in the identification of the proteins, such as myosin Ic, which contributions to adaptation.

The most extensively characterized sensory signaling cascade is phototransduction. In mice and humans, there are two types of photoreceptor cells that function in image-forming vision. The rods are highly sensitive to light and are the predominant photoreceptor cells used under low light conditions, while the cones are much less sensitive

and function in color vision. Phototransduction has been studied extensively in many vertebrate organisms, and as outlined in the review by Yingbin Fu and King-Wai Yau, studies in the mouse have lead to many breakthroughs because of the ability to combine electrophysiological, biochemical, and genetic approaches.

Drosophila phototransduction has also been the focus of numerous studies, and as Tao Wang and I describe, the founding member of the TRP superfamily emerged from analyses of fly vision. However, a longstanding conundrum is that there are major differences between *Drosophila* and mammalian phototransduction. Light activation of rods and cones leads to a drop in cGMP levels and closure of the cGMP-gated channels, while activation of fly phototransduction causes hydrolysis of phosphatidylinositol 4,5-bisphosphate and opening of the TRP channels.

During the last few years, it has become clear that there exists a third class of photoreceptors in mammals, which appear to operate through a cascade that has striking parallels with *Drosophila* phototransduction. As reviewed by David Berson, a small percentage of mammalian retinal ganglion cells are intrinsically photosensitive (ipRGCs) and are required for several nonimaging forming functions, including light-induced pupillary constriction and photoentrainment of circadian rhythm. Interestingly, there are indications that the ipRGCs function through a phosphoinositide signaling cascade that culminates with the opening of channels that have biophysical features reminiscent of TRP channels.

Circadian rhythm represents one of the best illustrations of the interplay between the sensory input and behavior and is conserved in virtually all animals. A key feature of circadian rhythms is that once the animals are entrained, they continue to display the same daily changes in behavior in the absence of the sensory input that initially set the cycle. The review by Ben Collins and Justin Blau describes many of the seminal discoveries on this topic that were made using *Drosophila* genetics. Most notably, the negative feedback loop that comprises the circadian clock is reviewed.

An exciting area of continuing investigation concerns the dissection of the mechanisms through which one sensory modality can influence another. Some of these intermodal interactions appear to function peripherally, such as through TRP channels that can respond to both thermal and chemical inputs. However, in other cases, the underlying mechanisms appear to be controlled through integration in the central nervous system rather than in the receptor cells. Finally, although the current special issue focuses on the reception and transduction of sensory input, an area of equal interest and active investigation concerns the mechanisms through which the brain decodes the myriad of sensory stimuli, such as the discrimination of thousands of different odorants, and distinct thermal stimuli.