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A Sucker for Taste

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Title: How does an octopus arm taste?

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Abstract

Biology is entering a new era in which techniques honed in model systems can be applied to the expanding array of organisms with sequenced genomes. In this issue of *Cell*, van Giesen et al. (2020) characterize the molecular foundation of the touch-taste sensory system in octopus suckers.

The value of studying diverse systems

The tools for studying molecular mechanisms have until recently been limited to a handful of model organisms. However, advances in genome sequencing have opened the doors to studying the unique bases of novel characters in many living organisms, and biologists have been busy taking advantage of this new age of biodiversity research (e.g., Matthews and Vosshall 2020). It is a rare occurrence when the general molecular basis of a sensory system is first described, but that is precisely what van Giesen and colleagues present in their study about the octopus chemotactile sense.

Despite 500 million years of independent evolution, vertebrates and cephalopods have convergently evolved sophisticated neural structures with analogous functions (Shigeno et al. 2018). The *Octopus bimaculoides* reference genome sequence (Albertin et al. 2015) revealed many of the genes potentially involved in octopus nervous systems, including an expanded group of atypical acetylcholine receptor genes highly expressed in the octopus sucker. Using transcriptomics and whole-cell patch clamp, van Giesen and colleagues confirm that these genes encode what they call chemotactile receptors or CRs. CRs are expressed in specialized chemosensory cells found in the octopus sucker epithelium. A second population of cells in the sucker epithelium were found to be mechanosensory cells reliant on NompC for mechanotransduction. The impressive array of electrophysiological experiments carried out by van Giesen et al. demonstrate that through these two cell types, octopus suckers produce finely tuned electrical signals that likely allow discrimination between stationary and mobile objects, and between attractive and aversive substances (Figure 1). Overall, the findings are an exciting leap in describing the octopus chemotactile sensory system, and will generate many new questions about the neurobiology, evolutionary ecology, and behavior of these intriguing animals.

A unique afferent nervous system

Octopus suckers send sensory information through ganglia at the sucker base to an arm nerve cord hypothesized to be functionally analogous to the vertebrate spinal cord (Shigeno et al. 2018). van Giesen et al. establish that CRs play a central role in providing the raw input for sensory processing in these tissues. CRs, like the acetylcholine receptors from which they

evolved, appear to form both homomeric and heteromeric protein complexes, which should allow for an incredible degree of variation in ligand sensitivity. Indeed, van Giesen et al. demonstrate that different pairings of CR transcripts produce receptors that have distinct ligand sensitivities and ion permeation properties that could elicit neuronal firing, activate downstream signaling cascades, or both. While van Giesen and colleagues deeply investigate the electro-chemical properties of three CR genes, the octopus genome has more than 20 CRs, as well as nearly 100 additional uncharacterized sensory genes (Albertin et al. 2015). Many questions remain: how do CRs combine to shape chemosensory properties? Are CRs tuned to modulate specific signal transduction pathways? How are these signals integrated in the arm nerve cord to modify arm motion? Work by van Giesen et al. have set the stage for further inquiry into the molecular biology of semi-autonomous arm behavior in octopus.

A broad role for taste

The octopus chemotactile sensory system presents not only an important opportunity to compare the neurobiology of cephalopods and vertebrates, but also a new perspective from which to study the ecology and evolution of cephalopods. One line of inquiry could address potential plasticity in the chemotactile sense. For example, salmon olfactory systems imprint on chemicals present in their natal stream (Scholz et al. 1976) and cuttlefish imprint on their first food source (Darmaillacq et al. 2006), raising the possibility that octopuses could imprint on their environment. One might predict that octopus chemosensation is tuned to locally available prey, which would select for differences in chemosensation (through mutations or regulatory changes in CRs) across or perhaps even within species. Perhaps some prey or predators of octopuses have evolved to manipulate the touch-taste sense for their own benefit. Because many of the chemicals that van Giesen tested did not elicit responses from CRs, it would be useful, as the authors state, to determine what additional chemicals or surfaces modulate CRs.

Notably, van Giesen and coauthors find that cephalopod ink diminishes the excitability of octopus chemoreceptors in a similar fashion to how ink inhibits squid olfaction. This raises the question of how other cephalopods sense such compounds and whether or not they possess proteins with similar properties as CRs. Other cephalopods do not appear to use suckers to taste their environment (Hanlon and Messenger 2018), suggesting that they lack an analogous chemotactile sense, and potentially also the CRs that encode it. Genomes from six cephalopod species are publicly available (although only two are chromosome-level assemblies, and four are octopuses), so syntenic regions could be aligned and compared to estimate when CRs appeared. Unfortunately, without more genomic data from cephalopods, it could be some time before this question is answered.

Ion channels like nicotinic acetylcholine receptors are often highly conserved, with evolutionary rates similar to that of cytochrome b (Hille 2001). Nevertheless, duplication and/or co-option of ion channel genes has given rise to several fascinating and novel sensory systems including the electric organ (Zakon et al. 2006) and lateral line (Chou et al. 2017). van Giesen et al. contribute a beautifully detailed example of how gene duplication can generate novelty. Now researchers can more deeply explore not only the molecular biology of this system, but also the role that other factors such as behavior, development, and natural selection have played.

Conclusion

While we may never know what it's like to be a bat (Nagel 1974), or an octopus for that matter, defining the molecular mechanisms that these animals use to explore their environment will aid our imagination. Such major discoveries should also fuel our curiosity for what else remains hidden.

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Figure Legends

Figure 1. Octopus suckers possess chemosensory cells that respond to stimuli with tonic firing and mechanosensory cells that respond to stimuli with phasic firing. Signals from both of these cell types are likely integrated within the octopus arm nerve cord and brachial ganglia, resulting in the semi-autonomic arm behaviors that allow octopus to hunt for prey in places they cannot see.