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Moth Olfaction: A Model of Exquisite Sensitivity and Specificity

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Olfaction, the sense of smell, differs widely among animals in terms of sensitivity and specificity. The olfactory systems of most invertebrates have developed to a level of extreme sensitivity and specificity since these animals rely on smell as the principal sensory modality [1]. This enables these animals to identify minute concentrations of behaviorally relevant compounds. Of course, both sensitivity and specificity are critical for their survival. Sensation of female pheromone by the antennae of a male moth is a prime example of this. An important first step in moth olfaction is the sensation of the pheromone by the Pheromone Binding Protein (PBP) present in moth antennae. Research in molecular biology, biochemistry and structural biology has lead to the discovery of many of the mechanistic details of this perireceptor event in moth olfaction. An impressive volume of research work has been carried out on these small soluble PBPs from several different insect species [2-10]. It is absolutely amazing to unravel the mysteries of how pheromone loading and unloading is conveniently controlled by changes in pH. The odor molecule is loaded at high pH near the sensillar lymph of the antennae and unloaded at low pH near the olfactory neuron. The mechanism of this loading and unloading at relatively high and low pH is fascinating and is a testimony to the perfection in the work of Nature. The PBP makes sure that the hydrophobic odor molecule is comfortable by housing it in a hydrophobic pocket during this short trip. The entry and exit of the odor molecule is regulated by two grates located at opposite ends of this hydrophobic pocket [11]. Two histidine residues (His70 and His95) at one end of the pocket serve as one gate while the C terminus on the opposite end of the pocket serves as the other. When the odor molecule is loaded at high pH, the gate controlled by the C terminus is opened while the two neutral histidine residues stay close to each other shutting that gate at the opposite end. When the odor molecule is unloaded at low pH, gate controlled by C-terminus is closed while the other gate is opened due to the repulsion between the now protonated and positively charged histidine residues. The exit of odor molecule is accompanied by the entry of the C terminus to the pocket of the PBP.

The exquisite sensitivity of moth olfaction is possibly both at perireceptor and receptor levels. PBPs may play a role in the specificity although they can pick up (bind) other hydrophobic molecules. It has been demonstrated that for PBPs of two moth species, *Bombyx mori* (BmoriPBP) and *Antheraea polyphemus* (ApolPBP1), they each pick up/bind a hydrophobic molecule endogenous to the *E. coli* system where the recombinant proteins are expressed [11,12]. Thus purified recombinant ApolPBP1 at high pH remain loaded with the hydrophobic molecule unless this molecule is forced out either by lowering pH or through a procedure called delipidation where the protein at pH 4.5 is passed through a hydrophobic resin (Lipidex) that can trap the hydrophobic molecule. The first approach of lowering pH to 4.5 ejects the hydrophobic molecule out but both the protein and the hydrophobic molecule remain in the same solution. That is if the pH were changed to above 6.0, the hydrophobic molecule would find its way into the hydrophobic binding pocket in PBP meant for pheromone molecule. The second method along with ejection of the hydrophobic molecule at low pH removes this molecule when passed through the Lipidex column.

Interestingly, the same phenomenon is seen for *Amyelois transitella* PBP1 (AtraPBP1) at pH 4.5 [13]. It has been reported that delipidation of AtraPBP1 at pH 4.5 has no effect on the protein. This is consistent with the above observation with ApolPBP1, where the endogenous hydrophobic molecule from *E. coli* system is automatically ejected at pH 4.5. Thus, in the case of AtraPBP1 whether the hydrophobic molecule was separated out through Lipidex resin or not (i.e. delipidation), has no effect on protein conformation at this lower pH since the protein at an acidic pH is not bound to these molecules as shown previously by Katre et al. [11]. However, delipidation will have an effect on the protein structure if the pH is raised to above 6.0. The protein at pH > 6.0 would pick up the hydrophobic molecules in solution unless they are removed from the protein solution using the Lipidex resin as illustrated for ApolPBP1 by Katre et al. [11].

In conclusion, moth olfaction involving pheromone signal is very fascinating. Although some selectivity may still be attributed to the perireceptor events, a clear understanding of the mechanisms of signal transduction at the receptor level is very critical. Investigation of the mechanisms of receptor activation is the next frontier to achieve to unravel the secrets of the exquisite sensitivity and selectivity of moth olfaction.

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