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Smells like evolution: the role of chemoreceptor evolution in behavioral change

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In contrast to physiology and morphology, our understanding of how behaviors evolve is limited. This is a challenging task, as it involves the identification of both the underlying genetic basis and the resultant physiological changes that lead to behavioral divergence. In this review, we focus on chemosensory systems, mostly in *Drosophila*, as they are one of the best-characterized components of the nervous system in model organisms, and evolve rapidly between species. We examine the hypothesis that changes at the level of chemosensory systems contribute to the diversification of behaviors. In particular, we review recent progress in understanding how genetic changes between species affect chemosensory systems and translate into divergent behaviors. A major evolutionary trend is the rapid diversification of the chemoreceptor repertoire among species. We focus mostly on functional comparative studies involving model species, highlighting examples where changes in chemoreceptor identity and expression are sufficient to provoke changes in neural circuit activity and thus behavior. We conclude that while we are beginning to understand the role that the peripheral nervous system (PNS) plays in behavioral evolution, how the central nervous system (CNS) evolves to produce behavioral changes is largely unknown, and we advocate the need to expand functional comparative studies to address these questions.

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Introduction

Finding food or mates, avoiding predation, or choosing a site to lay eggs all depend on the perception of and response to diverse environmental cues. Adapting behaviors is therefore a critical component of evolutionary success. How an organism interacts with its environment can be divided into three parts: first, the sensory perception of diverse auditory, visual, tactile, chemosensory or other cues; second, the processing of this information by the central nervous system (CNS), leading to a representation of the sensory signal; and third, a behavioral response. Thus, behaviors could evolve either through changes in the peripheral nervous system (PNS) (e.g. [1•]), or through changes in higher-order neural circuitry (Figure 1). While the latter remain elusive, recent work on chemosensation in insects illustrates how the PNS shapes behavioral evolution.

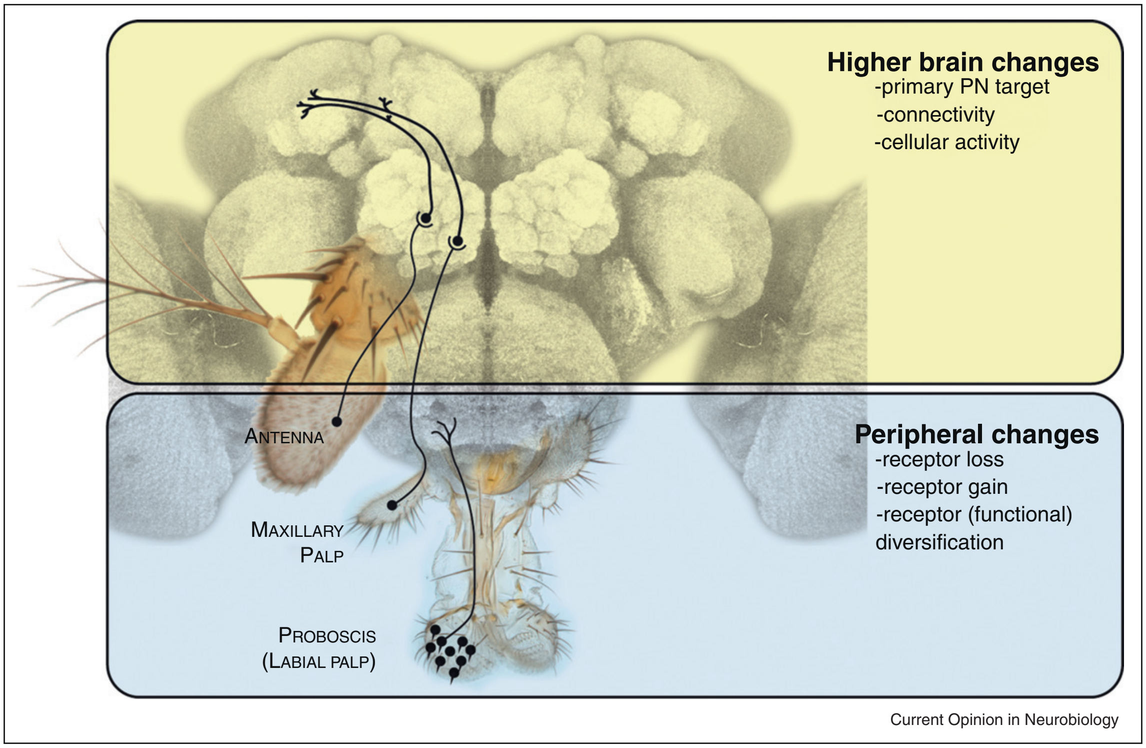
Chemosensation in insects depends on three classes of receptors expressed in peripheral neurons housed in specialized sensilla [2–4]. Olfaction depends on the insect-specific odorant receptors (ORs) on the antennae and palpae [2], as well as the more ancient ionotropic receptors (IRs) expressed in the antennae [4]. ORs vary rapidly between species, while IRs tend to be conserved across insect orders, possibly representing an ancestral insect chemodetection module for environmental cues of general interest [5,6•]. Gustation is mediated by gustatory receptors (GRs) housed in taste sensilla concentrated around the mouthparts, but also scattered throughout the body [7].

These receptors for chemosensation are evolving quickly, both in number and identity. For example, the number of IRs in protostome species ranges from 3 in *Caenorhabditis elegans*, to 85 in *Daphnia pulex* [5]. While this number is more stable across *Drosophila* species (58–66), phylogenetic analysis indicates tens of gains and losses in this genus [5]. The same pattern holds for ORs [8] and GRs [9•]. In all cases, there is extensive lineage-specificity of protein family members; for instance, only a handful of GRs are conserved even across flies [9•]. Clearly, the chemoreceptor families are gaining and losing genes all the time. Is this just neutral drift under a 'birth and death' model of gene family evolution [9•,10], or are there examples of gain, loss or diversification of chemoreceptors associated with changes in behavior?

Gain of chemoreceptor-encoding genes

There are several potential mechanisms by which a novel chemoreceptor could be added to an organism's preexisting sensory repertoire to change behavior. Neural circuits are defined not only by the actual wiring of interconnected cells, but also by the genes controlling the development of those cells, their activity, and for the

Figure 1



Possible levels of neuronal changes leading to divergent behaviors. In theory, changes in the nervous system leading to a divergent output response between closely related species can occur at the level of perception (blue box) or at the level of signal processing (higher brain centers, yellow box). In this review, we examine evolutionary examples of such changes in the context of chemosensation.

PNS, what chemoreceptors are expressed. While each OR is expressed in a single neuron [11], the neurons housing GRs and IRs typically express multiple receptor classes [4,12], allowing the expression of new chemoreceptors in a pre-existing cellular framework. Alternatively, new chemoreceptors might accompany additional changes at the cellular and genetic level.

The *Drosophila* IR84a receptor illustrates well how a novel chemoreceptor may modulate mating behavior through the integration of pre-existing neural circuits (Figure 2). IR84a is conserved in drosophilid flies, which court on food substrates, but is absent in other Dipterans, which do not [13••]. IR84a-expressing OSNs are activated by the fruit odors phenylacetic acid and phenylacetaldehyde. These sensory neurons express the male-specific courtship transcription factor Fru^M, and their activity is required for proper male courtship behavior. Importantly, wild type males, but not *IR84a* mutants, court more vigorously in the presence of IR84a ligands. Projection neurons downstream of this type of IR OSN typically innervate food odor-processing areas of the brain [13••,14]. Surprisingly though, the projection neurons downstream of IR84a-expressing OSNs innervate a pheromone-processing center, where they intermingle with other Fru^M-positive interneurons [13••,15]. Therefore, IR84a-mediated integration of food sensing circuits with the pre-existing Fru^M courtship circuitry may be responsible of the shift toward mating on food substrates in *Drosophila* species [13••].

A novel receptor may alter behavior by being expressed in pre-existing sensory neurons, and thus activate a downstream neural circuit in response to a new ligand. For instance, when the *D. melanogaster* receptor for the cVA pheromone, OR67d, was experimentally swapped for the *Bombyx mori* BmOR1 bombykol receptor, a normal cVA-mediated courtship suppression response was elicited with bombykol in these transgenic flies [16]. Similarly, ectopic expression of the GR64e glycerol receptor in CO_2 sensing neurons in the antenna was sufficient to confer glycerol sensitivity in these cells [17••]. One potential natural example of this process is the GR pxutGR1, which is expressed in the female legs of the swallowtail butterfly *Papilio xuthus* [18••]. Swallowtail butterflies are specialists, feeding and laying their eggs on specific host plants whose identity they check by drumming on the leaves with their forelegs [19]. PxutGR1 is the receptor for synephrine, one of 10 oviposition stimulants known for *P. xuthus*, and *pxutGR1* RNAi butterflies drum but fail to lay eggs on artificial leaves soaked in synephrine [18••]. While this example awaits comparative work, it is easy to envisage how changing the suite of GRs expressed on the