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Plasticity Mechanisms at the Peripheral Stage of the Olfactory System

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Abstract

Given the crucial involvement of olfaction in vital behaviors, the olfactory system has given priority to the functioning sustainability and robustness throughout the phylogenetic evolution. In addition, given the limitless and constantly changing number of potential stimuli, the olfactory system also gave priority to plasticity. Such priorities may account for some of exceptional adaptation skills which are expressed from the periphery. Manipulating the odorant environment has been an easy experimental way to study and evidence the olfactory system plasticity and has provided interesting insights into molecular mechanisms which maintain a robust, but plastic captors' system, to sample the chemical environment.

Keywords: Olfactory mucosa, Olfactory Receptors, Olfactory Sensory Neurons, Incidental induction, Plasticity, Training, Conditioning

Introduction

The olfactory system per se comprises three main levels, which are the olfactory mucosa (OM, i.e. the peripheral level) located in the nasal cavities, the olfactory bulb (OB, first central relay) and the piriform cortex (primary cortical level). The nasal cavities comprise several turbinates (3 in Human, 4 in rat or mouse), which are lined with the the respiratory mucosa and OM. In terrestrial animals, the nose samples odorant molecules in the inhaled air. The crucial initial step which governs the odor perception is that of the interaction between odorant molecules with specialized receptors, expressed by the olfactory sensory neurons (OSNs) lying in the OM. Through our natural rhythm of breath, the odorant molecules are captured by the mucus covering the OM and then, reach the cilia of OSNs and bind with molecular odor receptors (ORs). In terrestrial animals ORs are devoted to airborne odorants. Over the animal kingdom, the number of gene encoding ORs varies between species.

Odors are very complex stimuli which are mainly raised by mixtures of odorant chemical compounds displaying different degree of volatility. The volatility is directly related to a substance's vapor pressure at a given temperature; substances with higher vapor pressure vaporizing more readily than a substance with a lower vapor pressure. Thus, for a given combination of odorant molecules, the compounds compete with each other for constituting the gaseous phase; this competition depending on both individual volatility properties and ratios in which, the compounds are present. Altogether this will result in a unique and precise fragrance of an odor item. The quasi infinite variety of odorant compounds and their combinations, combined with the wide range of their volatility properties imply that the olfactory system must be thus highly sensitive and highly adaptable to new items. Lastly, the olfactory system must be operating very early in the organism life since it intervenes in numerous survival behaviors like predator avoidance, the bounding of the young to the mother and foraging behavior which starts at birth by the nipple research [1].

In addition to having to face limitless and constantly moving stimuli, the peripheral olfactory system needs to regenerate. Indeed, in the nose, OSNs are in direct contact with the air of our external environment and can be damaged by thermal, chemical or pathogen agression. Such a deleterious exposition is compensated by the fact that these neurons are continuously and cyclically renewed along the life with no apparent synchrony in terms of proliferation, differentiation and neurogenesis [2]. Their median turnover is every 6-8 weeks, even if some OSN probably live a longer time as recently demonstrated, which strongly arguments for selective bias in their turn-over [3]. Such

a renewal capacity could keep the system in a homeostatic state through a strict conservative pathway, as ORs are mainly chosen stochastically among hundreds of possible [4] or instead can be paired with plasticity in expression of ORs, to better fit with a changing environment. During their maturation, neo-OSNs would be "educated" by the surrounding adult OSNs. Indeed, odor induced activities of the latter might direct their OR expression choice [5-7]; an established mechanisms which would ensure both continuation and plasticity. OR expression could also be modulated independently from the OSNs' cyclic renewal, by the olfactory environment, experience and internal parameters in vertebrates (for recent reviews, see Lucero et al., 2013; Bryche et al. [8]) as well as in invertebrates [9].

In this review, we chose to present data on olfactory enrichment rather than deprivation because results are difficult to interpret and sometimes counterintuitive; deprivation likely triggering compensatory mechanisms [10]. Peripheral experienced induction or imprinting In olfaction, a major issue that implements and modulates the perception and contributes to the immediate and long-term adaptation of organisms to their environment is plasticity, which occurs from peripheral captors, i.e. OSNs and ORs. However, much attention has been paid on plasticity mechanisms occurring in higher brain areas [11-14] and much less is known about peripheral mechanisms.

Perceptual olfactory plasticity, dealing with peripheral changes driven by experience, has been originally described in human adults, thanks to the works of Wysocki and collaborators in eighties: when patients displaying androstenone specific anosmia were exposed to androstenone for some minutes, three times a day during six weeks, they restored their perception to this odorant [15]. These changes have been termed "experienced incidental induction" or imprinting [16] and, because anosmia was suspected to result from genetic deficit in peripheral captors, they have been assigned to the olfactory system periphery. Wysocki and colleagues [15] had following theory: exposure to androstenone would result in sensitization of OSNs by stimulating and selecting the expression of specific ORs with higher odor-binding affinity. As proposed for androstadienone for which receptors of different affinities co-exist, changes in perceived odor quality would result from their differential activation upon repetitive exposures [17]. The periphery involvement has been then endorsed in experiments reporting that chronic exposures to odorants increased the peripheral olfactory responses (measured through electro-olfactograms, EOG) in anosmic/hyposmic mice and humans [18,19]. More recently, olfactory training [20- 22] and aversive learning in humans (Cavazzana et al. 2018) have been shown to increase OSNs' responses and olfactory performances for conditioned stimulus, in normosmic, hyposmic or anosmic subjects. Noteworthy is that conditioning has probably stronger impacts on inherent experience-dependent olfactory performances than passive exposure.

However, because these studies are mainly concerned with anosmic or hyposmic subjects and animals, and rely to a limited number of odorants in conditions which are rarely natural, one may wonder whether such a phenotypical plasticity of peripheral neural responses and perception is a general phenomenon.

How Perceptual plasticity linked with functional changes at captors' level is generalizable

A piece of response lies in literature gathered in both invertebrates and vertebrates. After 10 days in water odorized with phenyl ethylic alcohol (PEA), salmons displayed a place preference for that water and an increased OSN responsiveness to PEA [16]. Similarly, in zebrafish, early exposure to PEA results in long-term changes in the number of neuronal precursors and in the level of expression for a subset of ORs [23,24]. In honeybees, pairing linalool and 9-oxo-decenoic acid (queen pheromone) with glucose reward down-regulated the expression of two ORs (the generalist OR 151 responding to linalool and the pheromone specific OR11), while peripheral electro-antennograms (EAGs: populational response of OSNs in insects, equivalent to EOGs in vertebrates) to these odorants were reduced [25] by contrast, similar learning of odor mixtures led to increased [26,27] or constant EAGs [28,29].

In rats, the voltage-die-sensitive peripheral response to a conditioned stimulus (CS) increased after conditioning [30]. In addition, early olfactory enrichment using daily exposure to multiple odorants increased OSNs' reactivity, both to previously experienced odorants and to novel ones [31].

In mice, effects of odorant exposure on ORs' number and sensitivity are contradictory depending on the context (either passive or active, via a positive or negative associative learning, through a continuous or discontinuous exposure). Indeed, mice passively exposed to octanal showed peripheral desensitization to CS (decreased in EOG amplitude) as well as behavioral habituation and down-regulation of proteins involved in peripheral transduction [32]. In mice passively exposed to lyral, the number of OSNs expressing MOR23 was down-regulated, while the remaining MOR23 endowed-OSNs expressed a higher density of this OR and increased excitability to lyral without impacting EOGs [33]. By contrast, aversive or fear learning or -place preference conditioning using odorant as CS enhanced both peripheral and behavioral responses [34-36]. Moreover, associative conditioning increased OSNs' excitatory outputs towards the olfactory bulb (OB) and detection abilities for CS [37]. More especially, such experiments increased CS-dedicated ORs' number and transmitter release probability from activated OSNs, enlarged glomerular size, reduced OB presynaptic inhibition mediated by $GABA_b$ receptors [34,38] and the incidence of lateral inhibition in OB interneurons; this latter effect can even lead to a lesser discrimination resulting in a generalization of the fear reaction to several nearby stimuli [39]. Such effects can be either reversed following extinction training [40] or persist over time and can even be transmitted to the next generation, through still unknown mechanisms [41]. When performed in the perinatal period, which could be assumed to a positive associative learning due to motherly presence, odor

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exposure also influences glomerular refinement and functioning with contrasted effects on OSNs/ORs numbers and epithelium responsivity [33,42,44-47]. Therefore, in both juvenile and adult animals, olfactory imprinting can induce changes in odor peripheral processing and perception. However, the perinatal period seems to be particularly sensitive to remodeling, thanks to a critical period for OSNs' axon wiring of the olfactory bulb (OB), in mice from birth to weaning [48-50].

Other experiments did not experimentally manipulate the olfactory environment of animals but reported observations linked to natural changing in chemical environments, linked to season changes, feeding states or breeding period. Thus, European starlings show seasonal differences in their ability to respond to odor cue [51]. In Drosophila, the expression of chemoreceptor genes such as OBPs proteins was shown to change with age, reproductive state and social interaction [52]. In the mosquito, blood meals were shown to induce a general reduction in antennal transcript levels of chemosensory genes, although a subset of ORs was modestly enhanced after feeding [53]. In honeybees, some results suggested that scent environment may regulate floral scent perception in honeybees [54]. Although none of these study have investigated odor learning and olfactory receptor expression per se, they support that experience-induced olfactory receptor plasticity is likely a phenomenon occurring in all animals that should manage changing odor environments.

Mechanisms Underlying Plasticity in OR Expression

These mechanisms have been mostly studied in animals, insects and rodents and recent experiments done in invertebrates and vertebrates established a clear relationship between changes in perception and OR expression. In insect, when submitted to an olfactory learning paradigm consisting in pairing the queen pheromone with glucose reward, the expression of the specific OR was downregulated while the peripheral OSN global electrophysiological response was reduced [25]. Although down-regulation of some ORs following odor chronicle passive exposition intuitively makes sense, it may seem counter-intuitive during memory formation resulting from an olfactory learning. However, a reduced number of ORs can be sufficient for the detection of familiar odorant. Correspondingly, it would be advantageous to have other ORs comparatively up-regulated; for example, to ensure that new floral scents are detected, allowing honeybees to adapt to their ever-changing scent environment [55,56].

The observed modulations in single or populational OSNs' responses to environmental stimulation could result from various mechanisms that are starting to be deciphered. As olfactory imprinting should be considered in light of activity-dependent survival as for other neuronal systems, it becomes clear that olfactory experience influences not only the survival but also the density of OSNs in the mucosa [57-60]. But, as mentioned in the previous section, effects of environmental exposure to single odorants, often used at high concentrations, are not always clear, OSNs' number or OR expression level being either increased, decreased or sometimes stable [33,42-44-47]. Few experiments have been conducted by manipulating complex but "natural" environments: when male and female mice are housed separately for an extended period, substantial differences in OR expression and OSN abundance are observed, most specifically for sexually dimorphic odors [61].

Two recent reports reconcile most studies by showing that only a fraction of OSN subtypes are selectively regulated by olfactory stimulation, that not all the epithelial zones are concerned and that the method of exposure, discontinuous or continuous, could be critical for inducing a functional plasticity. Indeed, changes in OSN repertoire abundance [62] as well as, birth rates of neurons expressing given ORs [63], would be highly dependent on olfactory stimulation type, occurring only when it is discontinuous. Along this line, in rabbit neonates, conditioned using mammary pheromone odorant [64], the increase of OSNs' response to CS supports an increase of either the density of ORs dedicated to CS processing or of the number of OSNs expressing such ORs (mainly through an activity dependent orientation in OR selection in newly mature OSNs) or both.

Thus, given the diversity of protocols and animal species which originated the studies of incidental induction, it is difficult to draw a general pattern. However, the analysis of the literature currently leads to consider induction as a generic phenomenon, with a "positive side" (enhancement of olfactory abilities) that would mainly occur after discontinuous exposure and/or conditioning, whereas passive and continuous exposure to odor cues would rather reveal a "negative side" (loss in olfactory reactivity or habituation). It can be proposed that such plasticity while, rather leading to a stronger processing of experienced reinforced stimuli, would drive the expression of the most adapted peripheral captors [65]; this selection could potentially lead to quantitatively reduce their number. In conjunction, the system would favour the detection of new odors (new experiences) at captor level. Such a hypothesis would be perfectly adapted to the olfactory system, a sensory system approached by a quasi-infinite number of stimuli. Moreover, olfactory training appears as a potent tool to increase as well as to restore specific olfactory abilities from the periphery [66]. Such a training effect can be then reinforced throughout activity-dependent associated events at the OB glomerular level, resulting in synaptic reorganization Cheethem & Belluscio [67]; Inoue et al. [68].

As a possible mechanism linking olfactory environment and OR gene expression, the epigenetic DNA modifications could participate to long-term large-scale neuronal plasticity in a controlled manner specific to each OSN. In mice, H2be, a histone variant which is overexpressed in inactive OSN, regulates their transcriptional program and shortens their life span [59]. A *de novo* DNA methyltransferase Dnmt3a is required for proper methylation of genes upon neuronal stimulation in OSN [69]. These epigenetic marks could also be involved in the transgenerational heritability of odor fear as observed by Dias & Ressler [41].

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Conclusion

As a conclusion, let us remember the sentence of Brennan & Keverne [70] who wrote "the olfactory system adaptability is extravagantly supported by the vast deployment of olfactory receptor's genes and neurogenesis phenomena" and let us add that the whole literature demonstrates that such a deployment is not vain because from the periphery, the olfactory function appears quite singular with regard to its incredible capacities of repair and functional adaptation [71].

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