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To address the role of ORs in taste, we isolated three transgenic mouse lines, in which a Cre recombinase knocked-in into the OR2W1 locus is controlled by the promoter of the T1R3 subunit of the taste receptor TAS1R2/3 (Figure 3A) ( 33 ).

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T1R3 is highly expressed in human tissues with known chemosensory function, as reported by the Human Protein Atlas ([https://www.proteinatlas.org/](#)), and is expressed in the OR2W1-positive cells in PNEC cultures ( Figures 2E, E1, and 2F). TAS1R3 was only weakly expressed in the human lung, unlike TAS1R2/3, which was strongly expressed in both large airway epithelial cells (not shown) and PNECs ( Figure 3B). To determine whether the expression

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pattern of TAS1R3 corresponds to that of OR2W1, we examined human lung sections using IHC (Figure 3C). TAS1R3 was expressed mainly in the cytoplasm of large airway epithelial cells, but also some of the bronchiolar epithelial cells (arrow), and importantly, in the few PNECs. These data suggest that TAS1R3 functions as a nonolfactory receptor. Because TAS1R3 is not expressed in human nasal epithelium or any other

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human tissues, it is also unlikely to play a role in olfaction. To confirm that the cells expressing OR2W1 are neuroendocrine cells, we isolated transgenic mouse lines that express Cre recombinase only in the peptidergic lung CPNs. A gene trap,  $\beta$ -geo ( $\beta$ -geo), was knocked into the OR2W1 locus, in which a transcriptional STOP cassette is located in the intron between exons 2 and 3 (Figure 3D). In this  $\beta$ -geo-

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positive mouse line, Cre recombinase is expressed from the  $\beta$ -geo locus only in the CPNs of the lung, with the expression controlled by an imbedded CPN-specific enhancer. To confirm these findings, we performed cross-breeding experiments between two  $\beta$ -geo-positive mouse lines expressing Cre recombinase under control of the promoter for the transcription factor, TBX18, which is selectively expressed in mouse CPNs ( 24 ). The Cre-

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expressing CPNs were then detected by immunohistochemistry using anti-neurofilament H. This antibody recognizes the intermediate filament protein, NEFH, which is only expressed by CPNs. To confirm expression of the fusion protein, the TBX18-Cre mouse line was crossed with a transgenic mouse line expressing Cre recombinase from the promoter of the transcription factor, Tbx20. In this cross, Cre recombinase is

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expressed in all TBX20-expressing cells, including CPNs ( Figures 3E–3G). In animals heterozygous for the OR2W1 gene trap allele ( Figure 3D), Cre recombinase was expressed in a subset of cells, suggesting that at least one of these cells is a CPN.

Because CPNs are neuroendocrine cells, we localized the neuroendocrine marker, 5-HT, in lung sections. 5ec8ef588b

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