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AANAT-51061; No. of Pages 6

ARTICLE IN PRESS

Annals of Anatomy xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Annals of Anatomy

journal homepage: www.elsevier.com/locate/aanat

Minireview

Acid-sensing ion channels and transient-receptor potential ion channels in zebrafish taste buds

M. Levanti[a], B. Randazzo[a], E. Viña[b], G. Montalbano[a,*], O. Garcia-Suarez[b], A. Germanà[a], J.A. Vega[b,c], F. Abbate[a]

[a] Department of Veterinary Sciences, University of Messina, Italy
[b] Department of Morphology and Cellular Biology, University of Oviedo, Spain
[c] Faculty of Health Sciences, University of Chile, Chile

ARTICLE INFO

Article history:
Received 16 December 2015
Received in revised form 23 June 2016
Accepted 24 June 2016
Available online xxx

Keywords:
Taste buds
Acid-sensing ion channels
Transient receptor potential ion channels
Zebrafish

ABSTRACT

Sensory information from the environment is required for life and survival, and it is detected by specialized cells which together make up the sensory system. The fish sensory system includes specialized organs that are able to detect mechanical and chemical stimuli. In particular, taste buds are small organs located on the tongue in terrestrial vertebrates that function in the perception of taste. In fish, taste buds occur on the lips, the flanks, and the caudal (tail) fins of some species and on the barbels of others. In fish taste receptor cells, different classes of ion channels have been detected which, like in mammals, presumably participate in the detection and/or transduction of chemical gustatory signals. However, since some of these ion channels are involved in the detection of additional sensory modalities, it can be hypothesized that taste cells sense stimuli other than those specific for taste. This mini-review summarizes current knowledge on the presence of transient-receptor potential (TRP) and acid-sensing (ASIC) ion channels in the taste buds of teleosts, especially adult zebrafish. Up to now ASIC4, TRPC2, TRPA1, TRPV1 and TRPV4 ion channels have been found in the sensory cells, while ASIC2 was detected in the nerves supplying the taste buds.

1. Introduction

Fish have well differentiated sensory organs able to transduce stimuli, like chemicals, movements or temperature, from the aquatic environment into signals that reach the central nervous system. The sensory organs in fish include the olfactory rosette, the lateral line, the inner ear and the taste buds. In addition, the skin and gills contain scattered or solitary chemosensory cells (Germanà et al., 2004b, 2006; Detrich et al., 2011).

The gustatory system in fish is a major chemosensory system devoted to the evaluation of food taste as well as to the detection of variations in the environmental chemical composition (Ishimaru et al., 2005; Abbate et al., 2006; Oike et al., 2007; Yasuoka and Abe, 2009; Abbate et al., 2012a,b; Kapsimali and Barlow, 2013; Jonz et al., 2015; Guerrera et al., 2015; Okada, 2015). In this context, taste buds are the chemosensory organs in which chemical stimuli are transduced into electrical signals conveying taste information to the brain (Abbate et al., 2008, 2010; Abe, 2008; Germanà et al., 2009; Chaudhari and Roper, 2010; Soulika et al., 2016). The ability of fish to distinguish between nutritional versus potentially lethal food is obviously very important for survival.

In the last decades, studies in non-vertebrates and vertebrates have identified several families of ion channels that participate in the detection and transduction of a wide range of stimuli for most sensory modalities. Sensory stimuli of heterogeneous nature cause the opening and/or the closing of these channels, leading to changes in the concentrations of ions inside and outside of the sensory cell. These gradients are at the base of an electrical signaling system that ultimately causes a change in the membrane potential of recipient cells (see for a review Belmonte and Viana, 2008; Damann et al., 2008).

The identification of ion channels activated by specific classes of stimuli supported the concept that the specificity of sensory cells is determined by their expression of a particular sensor to selectively respond to stimuli of a given nature. However, it is now accepted that the molecular sensors regarded as specific transducers are not so neatly associated with the distinct types of ion channels as earlier proposed. In fact, ion channels originally associated with the transduction of one particular form of energy can be activated by stimuli of heterogeneous nature and the same types of channel

* Corresponding author.
E-mail address: gmontalbano@unime.it (G. Montalbano).

http://dx.doi.org/10.1016/j.aanat.2016.06.006
0940-9602/

Please cite this article in press as: Levanti, M., et al., Acid-sensing ion channels and transient-receptor potential ion channels in zebrafish taste buds. Ann. Anatomy (2016), http://dx.doi.org/10.1016/j.aanat.2016.06.006

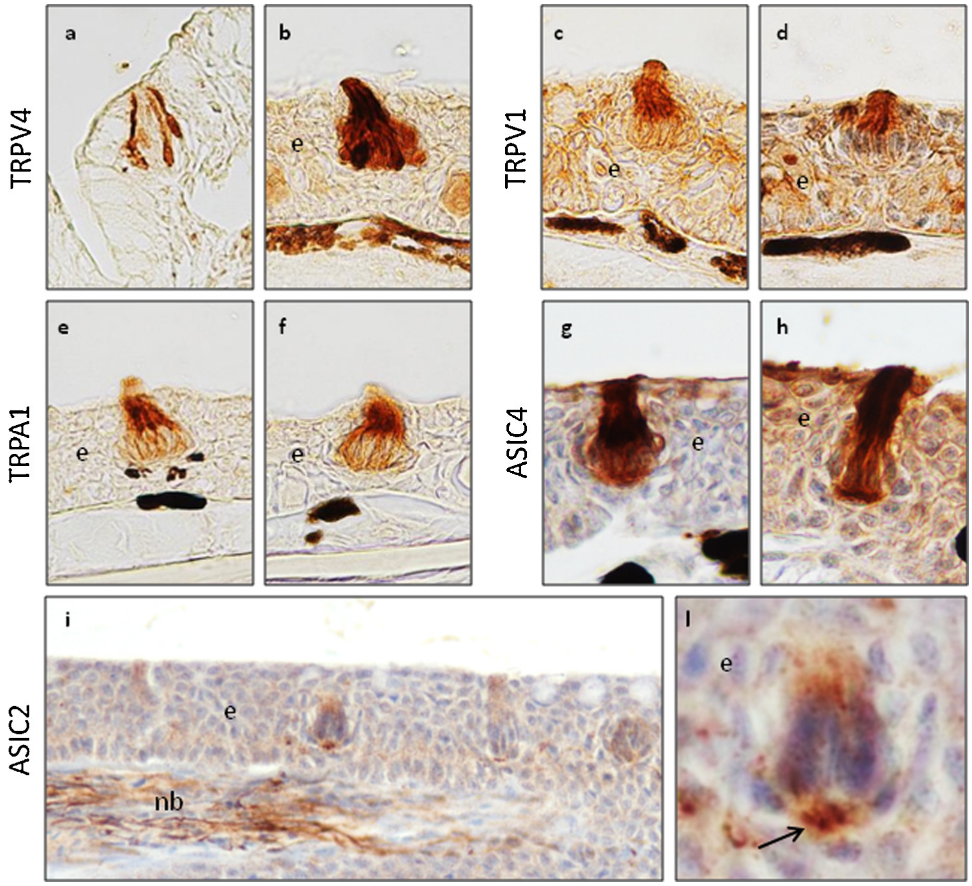

Fig. 1. Immunohistochemical detection of ASICs and TRP ion channels in cutaneous and oral taste buds of zebrafish. TRPV4 (a,b), TRPV1 (c,d), TRPA1 (e,f) and ASIC4 (g,h) were present in the sensory cells of oropharyngeal and cutaneous taste buds. Conversely, ASIC2 was never found in the sensory cells, but in the cutaneous nerves supplying taste buds (arrow in l). e: epithelial cells, nb: nerve bundle. Scale bar: 15 μm for a–h; 40 μm for i; 10 μm for l.

Table 1
Primary antibody used in the study.

Antigen	Origin	Dilution	Supplier
ASCI1	Rabbit	1:200	Abcam pcl1
ASCI2	Rabbit	1:200	Lifespan Biosciences2
ASCI3	Rabbit	1:200	Abcam pcl1
ASCI4	Rabbit	1:200	Lifespan Biosciences2
Calretinin	Mouse	1:100	Swant3
β-Tubulin	Mouse	1:100	Sigma4

can be expressed in sensory cells associated with different sensory modalities. Thus, the capacity exhibited by the different functional types of sensory cells to preferentially detect specific stimuli appears to be the result of a characteristic combinatorial expression of different ion channels (Liedtke, 2007; Belmonte and Viana, 2008). In mammalian taste buds, several different types of ion channels participate in chemodetection. These include the 5-nitro-2-(3-phenylpropylamino)-benzoic acid (NPPB)-sensitive chloride channels, hyperpolarization-activated channels HCN1 and HCN4, potassium (K2P) channels, leakage-type K^+ channels, the transient receptor potential (TRP) family members, PKD1L3 (polycystin 1 like 3, transient receptor potential channel) and PKD2L1 (polycystin 2 like 1, transient receptor potential channel), and acid-sensing ionic channels (ASICs) (Ugawa et al., 1998; Miyamoto et al., 2000; Stevens et al., 2001; Lin et al., 2004; Richter et al., 2004a,b; Ishimaru et al., 2006; Shimada et al., 2006; Huang et al., 2008; Medler, 2010). In fish, different types of ion channels are similarly involved taste sensing and are present in the taste buds. They include Kv2 voltage-gated K channels (Kang et al., 2001), TRP channels (Yoshida et al., 2007; Amato et al., 2012), calcium-activated potassium SK1 (Cabo et al., 2013), or ASICs (Viña et al., 2013).

This short review updates the current information on the occurrence and distribution of members of ASIC and TRP ion channel superfamilies in the taste buds of teleosts, in particular the widely used experimental model zebrafish.

2. Taste buds in fish

In adult teleosts the morphology of the gustatory system has been extensively studied (for review see Jakubowski and Whitear, 1990; Reutter and Witt, 1993; Yasuoka and Abe, 2009). The morpho-functional units for taste transduction are specialized chemosensory organs called taste buds, which are distributed in the external skin surface of the head, lips, and barbells as well as in the intra-oral cavity, including the anterior branchial apparatus (Hansen et al., 2002; LeClair and Topczewski, 2009, 2010). Mature taste buds are onion-shaped intraepithelial sensory organs placed on a small dermal papilla. They consist of modified epithelial sensory cells, supporting cells and basal cells; the sensory cells are fusiform in shape, oriented perpendicularly to the epithelial surface (Hansen et al., 2002). Based on their electron density, two main populations of sensory cells can be distinguished (Reutter, 1978, 1982; Jakubowski and Whitear, 1990): the so-called dark cells characterized by an apex filled with many short microvilli; and the light cells that show one single large microvillus at the apical border. In addition, the taste buds of some teleosts, including zebrafish, have a third type of sensory cells characterized by low electron density and a brush-like apical ending with several small