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Invited review

Acid-Sensing Ion Channels and nociception in the peripheral and central nervous systems

Emmanuel Deval ^{a, b, c, *}, Eric Lingueglia ^{a, b, c}

^a CNRS, Institut de Pharmacologie Moléculaire et Cellulaire (IPMC), UMR 7275, 06560 Valbonne, France

^b Université de Nice Sophia Antipolis, UMR 7275, 06560 Valbonne, France

^c LabEx Ion Channel Science and Therapeutics, UMR 7275, 06560 Valbonne, France

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ABSTRACT

Since their molecular cloning in the late 90's, Acid-Sensing Ion Channels (ASICs) have been shown to be involved in many aspects of nociception, both in peripheral and central neurons. In rodents, the combination of specific or non-specific pharmacological modulators of ASICs, together with *in vivo* knockdown and/or knockout animals has revealed their contribution to the detection, the modulation and the sensitization of the pain message by primary and secondary sensory neurons. Functional ASICs are homo or heterotrimers of different homologous subunits (ASIC1-3). Channels containing ASIC3 or ASIC1 subunits, appear to be important in peripheral nociceptors, where they are subject to intense regulation, while ASIC1a-containing channels also have a prominent role in central neurons, including spinal cord neurons that modulate and transmit the pain signal to the brain. In humans, experiments performed in healthy volunteers using drugs already used in the clinic and acting as poorly-selective inhibitors of ASICs, together with recent *in vitro* data obtained from stem cell-derived sensory neurons both support a role for these channels in nociception. These data thus suggest a real translational potential in the development of inhibitory strategies of ASICs for the treatment of pain.

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1. Introduction

The first reports of proton-induced depolarizing sodium currents in sensory neurons came from the pioneering work of Krishtal and colleagues (Krishtal and Pidoplichko, 1981a) who suggested a key role for these channels in nociception (Krishtal and Pidoplichko, 1981b,c) (see the review by O. Krishtal in this special issue, Krishtal, 2015). The molecular basis of these currents remained however controversial until the cloning of Acid-Sensing Ion Channels (ASICs) in the late 90's (Waldmann et al., 1997b). Since then, a growing body of evidence has accumulated showing the important role of ASIC channels in nociception in both the peripheral and central nervous systems, which is the focus of this review. The biophysical properties of these channels are discussed in detail in another review by S. Gründer & M. Pusch in this special issue (Gründer and Pusch, 2015).

E-mail address: deval@ipmc.cnrs.fr (E. Deval).

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2. ASIC expression in the pain pathway

ASIC channels are largely expressed throughout the pain pathway, including peripheral and central neurons (Table 1). Most of the ASIC subunits (*i.e.*, ASIC1a and b, ASIC2a and b, and ASIC3) are present in rodent peripheral sensory neurons (Chen et al., 1998b; Mamet et al., 2002; Poirot et al., 2006; Voilley et al., 2001; Waldmann et al., 1997a), where ASIC1b and ASIC3 are almost exclusively expressed (Chen et al., 1998b; Waldmann et al., 1997a). ASICs have been detected in the soma and in the peripheral terminals of Dorsal Root Ganglia (DRG) neurons (Alvarez de la Rosa et al., 2002; Garcia-Anoveros et al., 2001; Price et al., 2000, 2001), but have not been detected (at least for ASIC1a and ASIC2a) in the central terminals in the dorsal horn of the spinal cord (Duan et al., 2007; Garcia-Anoveros et al., 2001).

Native ASIC currents in rat DRG neurons are mainly supported by ASIC1-type and ASIC3-type channels (Deval et al., 2011, 2008; Diochot et al., 2012; Mamet et al., 2002; Poirot et al., 2006). ASICs are also functionally expressed in the trigeminal (TG) (Yan et al., 2011) and nodose (NG) ganglia neurons (Sugiura et al., 2005). The levels of ASIC transcripts, including ASIC1a, ASIC1b, ASIC2a and

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^{*} Corresponding author. CNRS, Institut de Pharmacologie Moléculaire et Cellulaire (IPMC), UMR 7275, 06560 Valbonne, France.

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Table 1

Tissue expression profile of the six ASIC subunits. Detection in the different species has been done by at least one of the methods listed in brackets. Note that the list is certainly not exhaustive and does not include functional data (e.g., electrophysiological characterization of native ASIC currents). Expression in some tissues that is based on a limited number of approaches (e.g., RT-PCR only) probably needs to be further characterized and functionally validated. Immunolocalization and Western blot data are highly dependent on the quality of the antibodies being used. Protein and/or transcript detection does not always differentiate between variants a and b of ASIC1 and ASIC2.

ASIC1aLat. nouse and human pian (M. R.F./-R. SH, WB, HC)(1-) (1-) (1)R.r. nouse and human pian (M. R.F./-R. SH, WB, HC)(1) (13) (10) (13) (13) (13)R.r. nouse, guinea pig and human DRG. To and NC (MB, RT-/-R. SH, WB, HC)(1) (12) (12) (13) (13) (12) (12) (13)R.at and rabit reins (RT-/-R. SH, WB, HC)(20)R.at and rabit reins (RT-/-R. SH, WB, HC)(20)Human lang cipilihal cells (RT-/R. HC)(20)R. at and nouse tasts receptor cells (RT-/R. HC)(20)Human bane cells (RT-/R. HC)(20)R. at and mouse tasts receptor cells (RT-/R. HC)(20)Human gluons (RT-/R. MC)(20)Human gluons (RT-/R. MC)(20)Mouse and guinea pig NC (RT-/R. MC)(20)Mouse and guinea pig	Subunits	Tissue expression profile (methods of detection)	References
Rat. mouse and human spinal cord (norther blot, BL, RF-PC, BL, WB) (7) (13) (4) (17) (19) (28) Rat. mouse spinal cord (norther blot, BL, RF-PC, BL, WB, BL/C) (4) (12) (4) (17) (19) (28) Rat. mouse spinal cord (RF-PC, BL, WB, HC) (4) (12) (4) (12) Hanscroptic (RC, WB) (6) (14) Hanscroptic (RC, WB) (6) (14) Hanscroptic (RC, WB) (7) (14) Hanscroptic (RC, WB) (7) (14) Mouse immune cells (RF-PCR) (2) Hanscroptic (RC, WB, BL/C) (2) Hanscroptic (RF-PCR) (2) Human Bone cells (RF-PCR) (2) Human Bone cells (RF-PCR) (2) Mouse immune cells (RF-PCR) (3) Mouse cordinal taket receptor cells (RF-PCR) (3) Rat and mouse spinal cord (R, B, R, RF-PCR) (3) Mouse cordinal taket receptor cells (RF-PCR) (3) Rat and mouse spinal cord (R, B, R, RF-PCR) (2) Rat and mouse spinal cord (R, R, R, RF, R, R, WB, R) (4) </td <td>ASIC1a</td> <td>Rat, mouse and human brain (NB, RT-PCR, ISH, WB, IHC)</td> <td>(1-4)(7-9)(17)</td>	ASIC1a	Rat, mouse and human brain (NB, RT-PCR, ISH, WB, IHC)	(1-4)(7-9)(17)
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ASIC2aRat, mouse and human brain (<i>NB</i> , <i>ISH</i> , <i>NT</i> - <i>PCR</i> , <i>NB</i> , <i>IHC</i>)(2) (4) (7) (8) (17) (36)Rat, mouse and human brain (<i>NB</i> , <i>ISH</i> , <i>NT</i> - <i>PCR</i> , <i>NB</i> , <i>IHC</i>)(4) (7) (13) (14) (28)Rat and mouse sipial cord (<i>NB</i> , <i>ISH</i> , <i>NT</i> - <i>PCR</i> , <i>NB</i> , <i>IHC</i>)(4) (7) (13) (14) (28)Rat, mouse and rabit retina (<i>NT</i> - <i>PCR</i> , <i>ISH</i> , <i>NB</i>)(24) (25) (33)Mice spiral ganglion in the cochlea (<i>HC</i>)(26) (33)Rat astrocytes (<i>HC</i> , <i>NB</i>)(26) (33)Human bung epithelia cells (<i>RT</i> - <i>PCR</i> , <i>HC</i>)(20)Human bung epithelia cells (<i>RT</i> - <i>PCR</i> , <i>HC</i>)(21)Human bung epithelia cells (<i>RT</i> - <i>PCR</i> , <i>HC</i>)(21)Human bung epithelia cells (<i>RT</i> - <i>PCR</i> , <i>HC</i>)(23) (34)Rat callured vascular smooth muscle cells (<i>RT</i> - <i>PCR</i> , <i>HC</i>)(21)Human glomas (<i>RT</i> - <i>PCR</i>)(23) (34)Rat card mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and human brain (<i>NB</i> , <i>ISH</i> , <i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(3) (3-Rat and mouse spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(4) (5) (5)Human brain, spinal cord (<i>RT</i> - <i>PCR</i> , <i>IHC</i>)(4) (5) (5)Human brain,		Mouse cochlear hair cells (stereocilia) (ISH, IHC)	(31)
Rat, mouse and guinea pig DRG and NG (RI-PCR, ISH, WB, IHC) (4-)(7) (13) (14) (28) Rat, mouse and rabbit retina (RI-PCR, USH, UBC) (4)(7) (13) (14) (28) Mice spiral ganglion in the cochlea (IHC) (35) Rat astrocytes (IHC, WB) (16) Rat astrocytes (IHC, WB, IHC) (26) (33) Human bone cells (RI-PCR, WB, IHC) (26) (33) Human bone cells (RI-PCR) (26) (33) Human bone cells (RI-PCR, HC) (21) Rat catrocytes (IRI-PCR, HC) (23) Rat catrocytes (IRI-PCR, HC) (23) (34) Rat catrocit body (RI-PCR) (23) (34) Rat catrocit body (RI-PCR, HC) (23) (34) Rat and mouse spinal cord (RI-PCR, IHC) (23) (34) Rat and mouse spinal cord (RI-PCR, IHC) (30) Rat and mouse spinal cord (RI-PCR, IHC) (33) (24) Rat and mouse spinal cord (RI-PCR, IHC) (33) (24) Rat aste receptor cells (RI-PCR, IHC) (31) (27) (30) Rat and mouse spinal cord (RI-PCR, IHC) (34) (55) (51) (51) Rat and mouse spinal cord (RI-PCR, IHC) (34) (52) (11) (17) (37-42) (45-48) (52) (54) (56) Human brain, spiniol cord, tesis (RI-PCR, IHC) (34) (55) (34) </td <td>ASIC2a</td> <td>Rat, mouse and human brain (NB, ISH, RT-PCR)</td> <td>(2) (4) (7) (8) (17) (36)</td>	ASIC2a	Rat, mouse and human brain (NB, ISH, RT-PCR)	(2) (4) (7) (8) (17) (36)
Rat and mouse spinal cord (<i>NB</i> , <i>ISH</i> , <i>RT-PCR</i> , <i>NB</i> , <i>IHC</i>) (4) (25) (3) Rat, mouse and rabbit retinal (<i>RT-PCR</i> , <i>ISH</i> , <i>VB</i>) (24) (25) (3) Mice spiral ganglion in the cochlea (<i>IHC</i>) (35) Rat attrocytes (<i>IHC</i> , <i>WB</i>) (16) Rat microglia (<i>RT-PCR</i> , <i>WB</i> , <i>IHC</i>) (26) (33) Human house cells (<i>RT-PCR</i>) (20) Human ineg epithelia cells (<i>RT-PCR</i> , <i>IHC</i>) (21) Human giomas (<i>RT-PCR</i> , <i>IHC</i>) (23) (34) Rat cacitured vascular smooth muscle cells (<i>RT-PCR</i> , <i>IHC</i>) (30) Ast cast exceptor cells (<i>RT-PCR</i> , <i>IHC</i>) (30) Rat and mouses painal cells (<i>RT-PCR</i> , <i>IHC</i>) (30) Ast cast exceptor cells (<i>RT-PCR</i> , <i>IHC</i>) (31) (24) Rat and mouses painal cells (<i>RT-PCR</i> , <i>IHC</i>) (31) (24) Rat and mouses painal cells (<i>RT-PCR</i> , <i>IHC</i>) (31) (24) Rat and mouse ratina <i>RT-PCR</i> , <i>IHC</i>) (31) (24) Rat and mouse ratina <i>RT-PCR</i> , <i>IHC</i>) (31) (24) Rat and guinea pity vasqual and glossopharypeal ganglia (<i>IHC</i> , <i>RT-PCR</i>) (27) Rat and mouse ratina <i>RT-PCR</i> , <i>IHC</i>) (24) (25) (33) Ast and guinea pity vasqual and glossopharypeal ganglia (<i>IHC</i> , <i>RT-PCR</i>) (27)		Rat, mouse and guinea pig DRG and NG (RT-PCR, ISH, WB, IHC)	(4–6) (11) (27) (32) (36) (54)
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Mice spiral ganglion in the cochlea (<i>HC</i>) (35) Rat astrocytes (<i>HC</i> , <i>WB</i>) (16) Rat microglia (<i>RT-PCR</i> , <i>WB</i> , <i>HC</i>) (18) Human hone cells (<i>RT-PCR</i>) (20) Human hung epithelial cells (<i>RT-PCR</i> , <i>HC</i>) (20) Rat cultured vascular smooth muscle cells (<i>RT-PCR</i> , <i>HC</i>) (21) Human giomas (<i>RT-PCR</i>) (22) Rat carotid body (<i>RT-PCR</i> , <i>HC</i>) (23) (34) Rat carotid body (<i>RT-PCR</i> , <i>HC</i>) (30) ASIC2b Rat and mouse spinal cord (<i>RT-PCR</i> , <i>HC</i>) (30) ASIC2b Rat and mouse spinal cord (<i>RT-PCR</i> , <i>HC</i>) (31) (24) Rat and mouse DRC (<i>RT-PCR</i> , <i>HC</i>) (33) (24) Rat and mouse spinal cord (<i>RT-PCR</i> , <i>HC</i>) (33) (24) Rat and mouse and manna DRG, TG and MG (<i>NB</i> , <i>ISH</i> , <i>RT-PCR</i> , <i>HC</i>) (31) (25) Rat and mouse and rabit retina (<i>RT-PCR</i> , <i>HC</i>) (31) (24) Rat and guinea pity sagal and gloscopharyngeal ganglia (<i>HC</i> , <i>RT-PCR</i>) (31) (24) Rat and guinea pity sagal and gloscopharyngeal ganglia (<i>HC</i> , <i>RT-PCR</i>) (31) (25) Muse simuna DRG, TG and MG (<i>NB</i> , <i>ISH</i> , <i>RT-PCR</i>) (31) (25) Muse ind rubus envis (<i>RT-PCR</i> , <i>HC</i>) (22)		Rat, mouse and rabbit retina (RT-PCR, ISH, WB)	(24) (25) (33)
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Rat microgia (RT-PCR, WB, IHC) (18) Human bone cells (RT-PCR) (26) (33) Human bone cells (RT-PCR) (20) Rat cultured vascular smooth muscle cells (RT-PCR, IHC) (21) Human gliomas (RT-PCR) (23) Rat taste receptor cells (RT-PCR, IHC) (23) Rat carotid body (RT-PCR) (23) Rat carotid body (RT-PCR) (30) ASIC2b Rat and mouse spinal cord (RT-PCR, ISH) (17) (36) Rat and mouse spinal cord (RT-PCR, ISH) (14) (28) (17) (36) Rat and mouse pIKG (RT-PCR) (5) (6) (36) (5) (6) (36) Guinea pig NG and JC (RT-PCR, ISH) (33) (24) (33) (24) Rat and mouse reline (RT-PCR, ISH) (33) (24) (34) Ast taste receptor cells (RT-PCR, IHC) (34) (55) (35) (52) (54) (55) Human brain, spinal cord, testis (RT-PCR, IHC) (24) (25) (43) (27) Mouse chondrocytes and synoviocytes (RT-PCR, IHC) (24) (25) (43) (24) Mouse chondrocytes and synoviocytes (RT-PCR, IHC) (24) (25) (43) (24) Mouse chondrocytes and synoviocytes (RT-PCR, IHC) (24) (25) (25) <		Rat astrocytes (IHC, WB)	(16)
Human boxe cells (K1-PCR) (2b) (33) Human lung epithelial cells (KT-PCR) (20) Rat cultured vascular smooth muscle cells (KT-PCR, IHC) (21) Human gliomas (KT-PCR) (22) Rat taste receptor cells (KT-PCR, IHC) (30) Rat carotid body (KT-PCR) (71) (36) Rat and human brain (NB, ISH, KT-PCR, IHC) (14) (28) Rat and mouse spinal cord (KT-PCR, ISH) (31) (24) Rat and mouse spinal cord (KT-PCR, IHC) (33) (24) Rat taste receptor cells (KT-PCR, IHC) (33) (24) Rat taste receptor cells (KT-PCR, IHC) (33) (24) Rat taste receptor cells (KT-PCR, IHC) (34) ASIC3 Rat, mouse and human DRC, TG and NG (NB, ISH, KT-PCR, IHC) (34) ASIC4 Human brain, spinal cord, testis (KT-PCR, NB) (71) (13) (17) (137-42) (45-48) (52) (54) (56) Human brain, spinal cord, testis (KT-PCR, IHC) (34) (44) (55) Rat and guinea pig vagal and glossopharyngeal ganglia (IHC, KT-PCR) (27) Rat and guinea pig vagal and glossopharyngeal ganglia (IHC, KT-PCR) (24) (25) (43) Mouse chondrocytes and synoviocytes (KT-PCR, IHC) (44) (55) Mouse chondrocytes (MT-PCR, W		Rat microglia (<i>RT-PCR</i> , <i>WB</i> , <i>IHC</i>)	(18)
Human lung epithelial cells (<i>R1-PCR</i> , <i>HC</i>) (20) Rat cultured vascular smooth muscle cells (<i>RT-PCR</i> , <i>HC</i>) (21) Human gliomas (<i>RT-PCR</i>) (22) Rat carotid body (<i>RT-PCR</i>) (30) Astic Carotid body (<i>RT-PCR</i> , <i>HC</i>) (31) Astic Carotid body (<i>RT-PCR</i> , <i>HC</i>) (31) Astic Carotid body (<i>RT-PCR</i> , <i>FRP</i> , <i>SFH</i>) (14) (28) Rat and mouse pinal cord (<i>RT-PCR</i> , <i>SFH</i>) (31) Guinea pig NG and JG (<i>RT-PCR</i> , <i>ISH</i>) (33) (24) Rat and mouse DEG (<i>RT-PCR</i> , <i>ISH</i>) (33) (24) Rat tast receptor cells (<i>RT-PCR</i> , <i>ISH</i>) (33) (24) Rat and mouse DEG (<i>RT-PCR</i> , <i>ISH</i>) (33) (24) Rat and mouse DEG (<i>RT-PCR</i> , <i>ISH</i>) (33) (24) Rat and mouse DEG (<i>RT-PCR</i> , <i>ISH</i>) (33) (24) Rat and mouse DEG (<i>RT-PCR</i> , <i>ISH</i>) (33) (24) Rat and guinea pig vagal and glossopharyngeal ganglia (<i>IHC</i> , <i>RT-PCR</i>) (34) ASIC3 Rat mouse and rabbit retina (<i>RT-PCR</i> , <i>IHC</i>) (24) (25) (43) Mouse chondrocytes and synovicoytes (<i>RT-PCR</i> , <i>IHC</i>) (24) (25) (43) Mouse chondrocytes and synovicoytes (<i>RT-PCR</i> , <i>IHC</i>) (24) (25) (43) Mouse inneu ne cells (<i>RT</i>		Human bone cells (<i>RT-PCR</i>)	(26) (33)
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Initial agitoms (N1-PCR) (22) Rat carotid body (RT-PCR) (30) ASIC2b Rat and human brain (NB, ISH, RT-PCR) (17) (36) Rat and nouse spinal cord (RT-PCR, ISH) (14) (28) Rat and nouse spinal cord (RT-PCR) (5) (6) (36) Guine apig NG and JG (RT-PCR) (33) (24) Rat and mouse retina (RT-PCR, ISH) (33) (24) Rat and mouse retina (RT-PCR, NB) (33) (24) Rat and mouse retina (RT-PCR, NB) (31) (5-7) (11) (17) (37-42) (45-48) (52) (54) (56) Human brain, spinal cord, testis (RT-PCR, NB) (77) Rat and guine apig vagal and glosopharynogeal ganglia (IHC, RT-PCR) (24) (25) (43) Mouse and rabbit retina (RT-PCR, IHC) (24) (25) (43) Mouse and rabbit retina (RT-PCR, IHC) (24) (25) (43) Mouse and rabbit retina (RT-PCR, IHC) (24) (25) (43) Mouse and provide glosopharynogeal ganglia (IHC, RT-PCR) (24) (25) (43) Mouse and provide glosopharynogeal ganglia (IHC, RT-PCR) (24) (25) (43) Mouse and provide glosopharynogeal ganglia (IHC, RT-PCR) (24) (25) (43) Mouse and provide glosopharynogeal ganglia (IHC, RT-PCR) (24) (25) (43) Mouse intervide (RT-PCR, WB, IHC)		Rat cultured vascular smooth muscle cells (<i>R1-PCR</i> , IHC)	(21)
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ASIC2b Rat and human brain (<i>NB</i> , <i>ISH</i> , <i>RT</i> -PCR) (17) (36) Rat and mouse spinal cord (<i>RT</i> -PCR, <i>ISH</i>) (14) (28) Rat and mouse opinal cord (<i>RT</i> -PCR, <i>ISH</i>) (27) Rat and mouse retina (<i>RT</i> -PCR, <i>ISH</i>) (27) Rat and mouse retina (<i>RT</i> -PCR, <i>ISH</i>) (27) Rat aste receptor cells (<i>RT</i> -PCR, <i>IHC</i>) (3) (24) ASIC3 Rat, mouse and human DRG, TG and NG (<i>NB</i> , <i>ISH</i> , <i>RT</i> -PCR, <i>IHC</i>) (3) (5-7) (11) (17) (37-42) (45-48) (52) (54) (56) Human brain, spinal cord, testis (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (43) Rat and guinea pig vagal and glossopharyngeal ganglia (<i>IHC</i> , <i>RT</i> -PCR) (27) Rat, mouse and rabbit retina (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (43) Mouse chondrocytes and synovicoytes (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (43) Mouse chondrocytes and synovicoytes (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (43) Mouse chondrocytes (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (43) Mouse chondrocytes (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (43) Mouse chondrocytes (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (44) Mouse adipocytes (<i>RT</i> -PCR, <i>IHC</i>) (24) (25) (44) Mouse adipocytes (<i>RT</i> -PCR, <i>IHC</i>) (26) (26) Human lung epithelial cells (<i>RT</i> -PCR, <i>IHC</i>) (20) Human lung epithelial cells (<i>RT</i> -PCR, <i>IHC</i>) (20) Human lung epithelial cells (<i>RT</i> -PCR, <i>IHC</i>) (21) (26) Rat at adm couse taste receptor cells (<i>RT</i> -PCR, <i>IHC</i>) (23) (44) Mouse inner ear (<i>RT</i> -PCR, <i>IHC</i>) (23) (44) Mouse inner ear (<i>RT</i> -PCR, <i>IHC</i>) (30) ASIC4 Mouse base taste receptor cells (<i>RT</i> -PCR, <i>IHC</i>) (31) (26) Ast carotid body (<i>RT</i> -PCR, <i>IHC</i>) (30) AsIC4 Mouse inner ear and pituitary gland (<i>NB</i> , <i>RT</i> -PCR) (51) Mouse innume cells (<i>RT</i> -PCR) (51) Mouse innume cells		Rat laste receptor cens (RI-PCR, IHC)	(20)
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Rat and rabbit retina (<i>RT-PCR</i>) (24) (25)		Mouse immune cells (<i>RT-PCR</i>)	(19)
		Rat and rabbit retina (<i>RT-PCR</i>)	(24) (25)

<u>Abbreviations</u>: DRG: Dorsal Root Ganglia, TG: Trigeminal ganglia, NG: Nodose Ganglia, JG: jugular ganglia; NB: northern blot; ISH: in situ hybridization; IHC: immunolocalization; WB: Western blot; RT-PCR: Reverse Transcriptase – Polymerase Chain Reaction (quantitative or not).

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