

## Update article

“Interneurons” in the olfactory bulb revisited<sup>☆</sup>Toshio Kosaka<sup>a,\*</sup>, Katsuko Kosaka<sup>b</sup><sup>a</sup> Department of Anatomy and Neurobiology, Graduate School of Medical Sciences, Kyushu University, Higashi-ku, Fukuoka 812-8582, Japan<sup>b</sup> Department of Health Sciences, Graduate School of Medical Sciences, Kyushu University, Fukuoka 812-8582, Japan

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## ABSTRACT

The main olfactory bulbs (MOBs) are now one of the most interesting parts of the brain in at least two points; the first station of the olfaction as an excellent model for understanding the neural mechanisms of sensory information processing and one of the most prominent sites whose interneurons are generated continuously in the postnatal and adult periods. Here we point out some new aspects of the MOB organization focusing on the following 4 issues: (1) there might be both axon-bearing and anaxonic periglomerular cells (PG cells), (2) most parvalbumin positive medium-sized neurons in the external plexiform layer as well as a few nitric oxide synthase positive PG cells and calretinin positive granule cells are anaxonic but display dendritic hot spots with characteristics of axon initial segments, (3) some of so-called “short-axon cells” project to the higher olfactory related regions and thus should be regarded as “nonprincipal projection neurons” and (4) tyrosine hydroxylase positive GABAergic (DA-GABAergic) juxtglomerular neurons (JG neurons) are a particular type of JG neurons as a main source of the interglomerular connection, forming an intrabulbar association system.

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## 1. Introduction

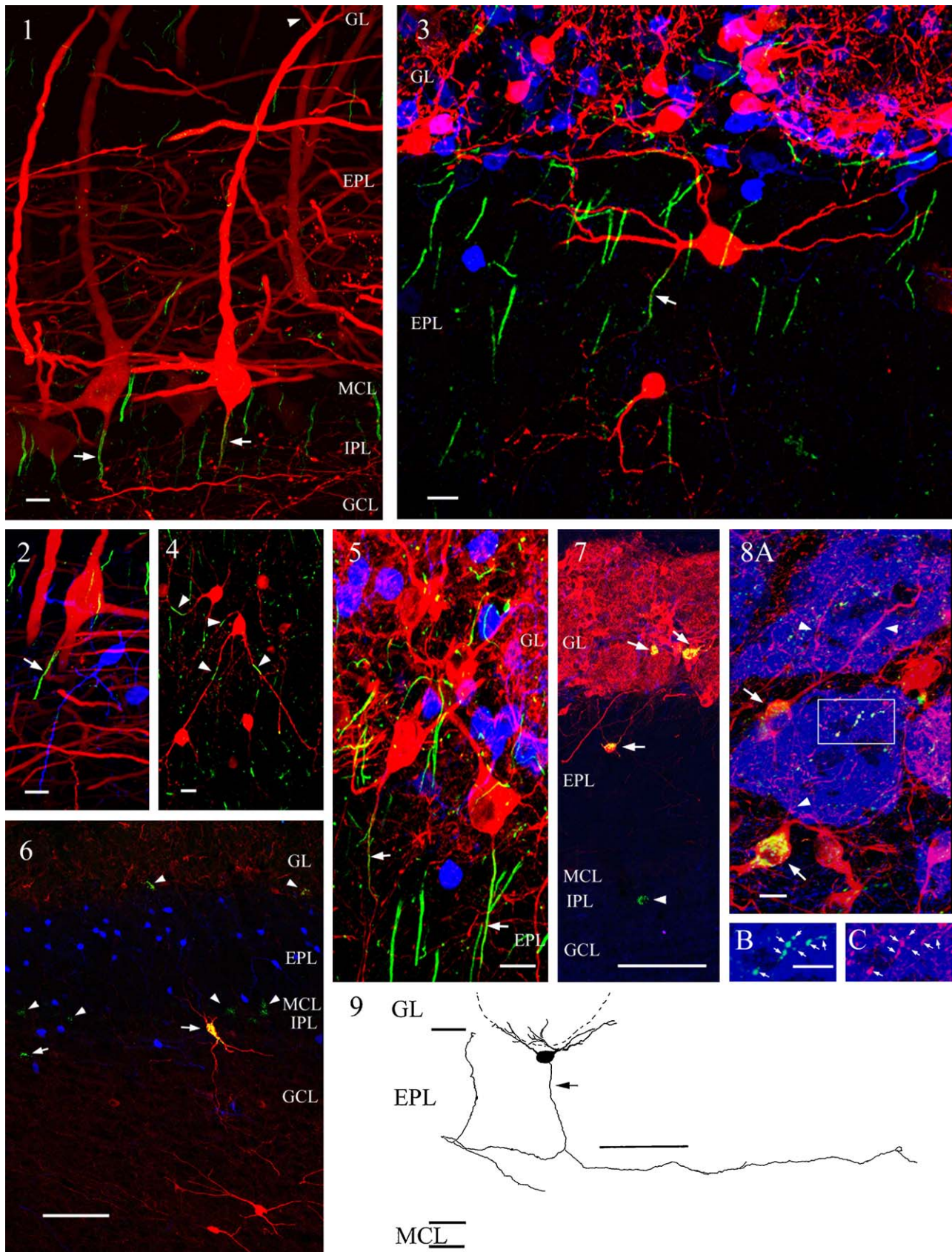
The main olfactory bulb (MOB) is the first relay station for transmission of olfactory information, which receives and processes the information from the olfactory sensory neurons in the nasal mucosa, and sends this information to different parts of the primary olfactory cortex in the forebrain. After the epoch-making study of Buck and Axel (1991), the MOB is considered as an excellent model for understanding the neural mechanisms of sensory information processing. The MOB is also attracting attention of many researchers for it is one of the most prominent sites whose interneurons are generated continuously in the postnatal and adult periods from the progenitor cells located in the subventricular zone (SVZ) of the lateral ventricle and migrate through the rostral migratory stream (Altman, 1969; Lledo et al., 2008). We reported a short summary of our data and our proposal on the glomerular organization and classification of periglomerular cells (PG cells) of the rodent MOB more than 10 years ago (Kosaka et al., 1998), in which

we proposed the compartmental organization of the glomeruli and two types of PG cells based on the intraglomerular dendritic arborization correlating with their chemical properties (Kosaka et al., 1997). We also reported some reviews on the structural organization of the MOB focusing on the subtypes of PG cells and the intraglomerular neuronal interactions via synaptic and gap junctional connections (Kosaka and Kosaka, 2005, 2009a). However, several new findings of our own and other groups on the organization of the MOB are now changing the previous concept of the MOB organization. In the present article, showing some of our supplemental data unpublished previously, we point out the following 4 issues. (1) There might be both axon-bearing and anaxonic PG cells. (2) Most parvalbumin (PV) positive medium-sized neurons in the external plexiform layer (EPL) as well as a few nitric oxide synthase (NOS) positive PG cells and calretinin (CR) positive granule cells are anaxonic but display dendritic hot spots with characteristics of axon initial segments (AISs). (3) Some of so-called “short-axon cells (SA cells)” project to the higher olfactory related regions and thus should be regarded as “nonprincipal projection neurons”. (4) Large tyrosine hydroxylase (TH) positive neurons, which had been regarded as external tufted cells but later revealed to be GABAergic (DA-GABAergic), are a particular type of juxtglomerular neurons (JG neurons) as a main source of the interglomerular connection, forming an intrabulbar association system. Here we had better to pay attention to the term “juxtglomerular neuron (JG neuron)”. To our knowledge the term “JG neuron” appeared to be first used in relation with TH positive neurons around glomeruli

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**Figs. 1–9. Fig. 1.** Pseudo-colored confocal laser-scanning light microscope (CLSM) partial projection image of biotinylated dextran amine (BDA)-labeled mitral cells (red) and axon initial segments (AISs) immunostained for  $\beta$ IV-spectrin (green) in the mouse MOB. BDA was injected iontophoretically into the external plexiform layer (EPL). Arrows indicate  $\beta$ IV-spectrin positive AISs of BDA-labeled mitral cells. Arrowhead indicates initial part of the glomerular dendritic tuft of the mitral cell primary dendrite. Layers: glomerular layer (GL), external plexiform layer (EPL), mitral cell layer (MCL), internal plexiform layer (IPL), granule cell layer (GCL). Scale bar is 10  $\mu$ m.

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