

Chapter 57

The Teleost Fish

Takanori Ikenaga

Abstract In vertebrates, the basic structure of the central nervous systems, including the cerebellum, is conserved from mammals to teleosts. The cerebellum of teleost fish is subdivided into three parts: the corpus cerebelli, valvula cerebelli, and vestibulolateral lobe. Although the existence of basket cells remains unconfirmed, the teleost cerebellum possesses intra cerebellar neurons that are similar to those of other vertebrates. Additionally, there are similarities in the pattern of connectivity of these neurons and the neurotransmitters that are used. In the teleost cerebellum, the structure corresponding to the deep cerebellar nuclei is absent. Instead, the teleost cerebellar efferent neurons do not make clusters and are distributed within the ganglionic layer, which is equivalent to the Purkinje cell layer of other vertebrates. Efferent neurons use excitatory neurotransmitters and project their axons outside of the cerebellum. These efferent neurons are unique to the teleost cerebellum, so a detailed understanding of their structure and function may yield important clues about the evolution and function of the teleost cerebellum. Afferent and efferent fiber connection patterns suggest that the basic functions of the teleost cerebellum are similar to those of other vertebrates, but each subdivision of the teleost cerebellum is functionally separated. The functional role of the teleost cerebellum is still not fully understood, but research suggests that the teleost cerebellum has an important role in the execution of swimming gait and emotional learning.

Keywords Corpus cerebelli • Valvula cerebelli • Caudal lobe • Teleost • Evolution • Goldfish • Efferent cell • Purkinje cell • Deep cerebellar nuclei • Neurotransmitter • Fiber connection • Motor control • Fair conditioning • Zebrafish • Actinopterygian fish

The actinopterygii (ray finned fish) includes approximately 27,000 species, the majority of which are teleost fish (approximately 26,800 species) (Nelson 2006). The basic organization of the central nervous system of teleost fish is similar to that of other vertebrates including the cerebellum. In this chapter, I review the

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morphology, cellular organization, fiber connections, and functions of the teleost cerebellum.

57.1 Morphology, Cellular Organization, and Neural Circuits of the Teleost Cerebellum

The cerebellum of teleosts is subdivided into three major parts: the corpus cerebelli, valvula cerebelli, and the vestibulolateral lobe (including the eminentia granularis and lobus caudalis) (Fig. 57.1). The corpus cerebelli, considered to be homologous

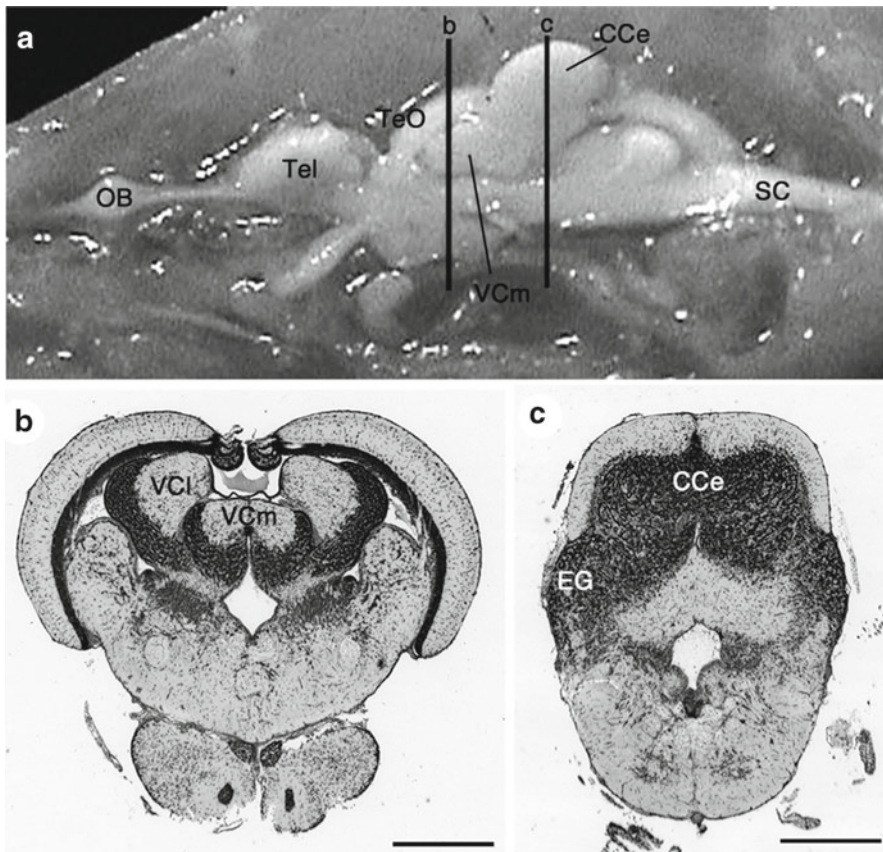


Fig. 57.1 (a) Mid-sagittal plane of the goldfish brain. (b, c) Transverse sections of the goldfish brain including the cerebellum through lines indicated in (a). *Abbreviations:* *CCe* corpus cerebelli, *EG* eminentia granularis, *OB* olfactory bulb, *SC* spinal cord, *Tel* telencephalon, *TeO* optic tectum, *VCl* lateral lobe of valvula cerebelli, *VCm* medial lobe of valvula cerebelli. Scale bar = 500 μm (Adapted from Ikenaga et al. 2006)

to the vermis of other vertebrates (Ito 1978), lies in the central portion of the teleost cerebellum and extends dorsally and curves either rostrally (e.g., mormyrids, catfish) or caudally (e.g., cyprinids, salmonids) (Fig. 57.1a, c). The valvula cerebelli is unique to actinopterygian fish and is not an obvious homologue of any cerebellar components of other vertebrates. It protrudes rostrally into the mesencephalic ventricle and is covered by the optic tectum (Fig. 57.1a, b). In some species, including goldfish, the valvula is subdivided into medial and lateral lobes (Fig. 57.1b). The vestibulolateral lobe consists of the eminentia granularis and lobus caudalis. In goldfish, the eminentia granularis is located in the ventro-lateral region of the corpus cerebelli as a granular cell mass (Fig. 57.1c). The lobus caudalis is an easily distinguishable structure in mormyrid fish, and protrudes from the caudal edge of the corpus cerebelli (Campbell et al. 2007). On the basis of its strong morphological relationship with the central lateral line sensory region, it is suggested that the vestibulolateral lobe is homologous with the tetrapodian flocculus (Meek 1992).

The teleost corpus cerebelli consists of three layers, which is consistent with the structure in other vertebrates (Fig. 57.1c). Parallel fibers from granule cells and dendrites of Purkinje cells represent the major components of the molecular layer of the teleost cerebellum. The presence of stellate cells has been reported (Nieuwenhuys et al. 1974; Han and Bell 2003), but to date there is no evidence to indicate the existence of basket cells in the teleost. The Purkinje cell layer in the teleost cerebellum is referred to as the ganglionic layer in some studies. This is because it contains both Purkinje cells and efferent cells termed eurydendroid cells (Meek 1992; Han and Bell 2003). The morphology of teleost Purkinje cells is basically similar to those of other vertebrates; one thick primary dendrite emerges from the apical part of the cell body and branches are distributed into the molecular layer and oriented sagittally. Axons of Purkinje cells of the corpus cerebelli run within the ganglionic layer and terminate onto the somata and main dendrites of the efferent cells (Nieuwenhuys et al. 1974; Ikenaga et al. 2005; Bae et al. 2009), and also onto other Purkinje cells (Meek and Nieuwenhuys 1991). The climbing fiber makes glutamatergic inputs onto somata or the proximal region of the primary dendrites of Purkinje cells, but does not climb to the distal section of dendrites, unlike in mammals (Han and Bell 2003). Efferent cells, another kind of neuron in the ganglionic layer, will be mentioned in detail later. The granule cell layer is located in the deepest portion of the teleost corpus cerebelli (Fig. 57.1c) and contains granule cells and Golgi cells.

57.2 Efferent Neurons of the Teleost Cerebellum

One unique feature of the teleost cerebellum is the lack of deep cerebellar nuclei. Instead, cerebellar efferent neurons are distributed in the ganglionic layer. The cerebellar efferent cells of teleost fish have two or more primary dendrites (Fig. 57.2) (Nieuwenhuys et al. 1974; Murakami and Morita 1987; Ikenaga et al. 2005). Like Purkinje cells, the efferent cells have an extensive dendritic arbor along the parasagittal dimension and are spread within the molecular layer. The shape of the efferent

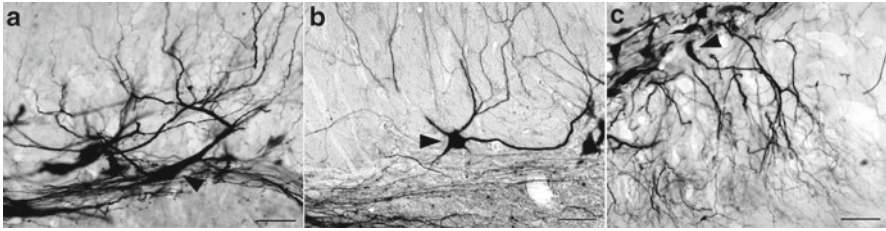


Fig. 57.2 Photomicrographs of retrogradely labeled cerebellar efferent neurons in the goldfish corpus cerebelli. (a) Fusiform type neurons. (b) Polygonal type neurons. (c) Monopolar type neurons. Arrowheads indicate cell bodies of efferent neurons. Scale bar = 50 μm (Adapted from Ikenaga et al. 2006)

cells can vary even within a single species; in goldfish, they are classified into three types according to their morphology (Fig. 57.2) (Ikenaga et al. 2005). The efferent cell dendrites have fewer spines than those of the Purkinje cells (Nieuwenhuys et al. 1974; Murakami and Morita 1987; Campbell et al. 2007). In the goldfish corpus cerebelli, large numbers of neurons in the ganglionic layer were labeled with anti-GABA antibody, but retrograde labeled efferent cells were not labeled with same antibody, suggesting that Purkinje cells utilize GABA as a neurotransmitter whereas efferent cells are mediated by different one (Ikenaga et al. 2005). In zebrafish, some efferent neurons strongly express *vglut2alb* mRNA (vesicular glutamate transporter), suggesting that teleost cerebellar efferent neurons are glutamatergic (Bae et al. 2009). The axons of Purkinje cells terminate onto the somata and the main dendrites of the efferent cells in the mormyrid corpus cerebelli (Nieuwenhuys et al. 1974). Experiments combining retrograde labeling and immunohistochemistry indicate that efferent cells receive GABAergic inputs from Purkinje cells in the goldfish corpus cerebelli (Ikenaga et al. 2005). This relationship between the efferent cells and Purkinje cells is similar to that between the deep cerebellar nuclei and Purkinje cells in the mammalian cerebellum. Therefore, teleost cerebellar efferent neurons have some similarities with neurons of the deep cerebellar nuclei of mammals. The information about the cerebellar efferent system used by other fish is not sufficient. There is a need for additional studies of the cerebellar efferent systems of other fish to gain further insight into cerebellar evolution in vertebrates.

57.3 Afferent and Efferent Fiber Connections

The teleost cerebellum receives inputs via climbing fibers and origin of them is in the inferior olive, as is the case in other vertebrates. Additionally, the corpus receives inputs from the diencephalon, pretectal area, mesencephalon, rhombencephalon, and spinal cord in goldfish (see detail in Wullimann and Northcutt 1988). The afferent source of the lateral lobe of the valvula in goldfish partially overlaps with that of the corpus (Wullimann and Northcutt 1989).

The efferent targets of the goldfish corpus cerebelli are also widely distributed and include the diencephalon, pretectal area, mesencephalon, and rhombencephalon (see detail in Wullimann and Northcutt 1988; Ikenaga et al. 2002). The efferent targets of the medial lobe of the valvula cerebelli are very similar to those of the corpus cerebelli. Conversely, the lateral lobe of the valvula cerebelli projects only to a limited area (see detail in Ikenaga et al. 2002). These observations suggest that the roles of the corpus and the medial lobe of the valvula include both motor control and functions carried out by the mammalian higher cerebellum. It is also suggested that there are functional divisions between the medial and lateral lobes of the valvula cerebelli.

57.4 Functions of the Teleost Cerebellum

Ablation of the corpus in rainbow trout resulted in individuals being unable to maintain a steady position and subsequently being swept backwards in fast flowing water, suggesting that the corpus cerebelli is essential for smooth shifts between different motor programs, but has no role in the generation of motor programs (Roberts et al. 1992). Matsumoto et al. (2007) reached a similar conclusion based on observations of the swimming performance of goldfish with a partially ablated corpus cerebelli. In addition to the function in motor control, recent studies also suggest that the teleost corpus cerebelli has a critical role in learning, memory, and cognition. Ablation of the corpus cerebelli of goldfish impairs classical fear conditioning and spatial cognition (Yoshida et al. 2004; Gómez et al. 2010). Additionally, local anesthetization of the corpus cerebelli with drug application resulted in similar impairment (Yoshida and Hirano 2010). In contrast to the corpus, little is known about the function of the valvula. The valvula is covered by the optic tectum (Fig. 57.1), so is difficult to ablate without damaging other brain regions. To address this issue, genetic manipulation of the nervous system using zebrafish or medaka which is known as model animal must be useful. The combined application of new techniques and traditional electrophysiology and behavioral analysis continues to improve our understanding of the function of the teleost cerebellum.

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