



**Descending pathways to the spinal cord in teleosts in comparison with mammals, with special attention to rubrospinal pathways**

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8 Descending pathways to the spinal cord in teleosts in comparison with  
9 mammals, with special attention to rubrospinal pathways.  
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**Abstract**

In this article we review descending neural pathways to the spinal cord in teleosts, comparing with mammals. Descending pathways to the spinal cord are crucial in controlling various behavior in vertebrates. The major difference between teleosts and mammals is the lack of corticospinal (or palliospinal) tracts. Other descending pathways, which originate from the brain stem, are basically identical in teleosts and mammals. This suggests the presence of common systems in the spinal motor control by higher order centers. The homologue of nucleus ruber remained unclear in teleosts until recent, and this review pays special attention to the rubrospinal tract.

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## Introduction

Descending pathways to the spinal cord exerts regulatory influences on spinal neurons. One of the most important roles of the pathways is the control of behavior. Abundant knowledge on the descending pathways has been accumulated in mammals. In mammals, corticospinal, rubrospinal, tectospinal, interstitiospinal, reticulospinal, and vestibulospinal tracts are the major descending pathways involved in motor control (Nieuwenhuys *et al.* 1988; Steward, 2000; Martin, 2003). Recently, zebrafish and medaka have become major model vertebrates, and studies have been performed in various fields such as developmental biology and neuroscience. However, much remains to be studied regarding neuroanatomical substrates involved in the motor system of teleosts including zebrafish and medaka. In this article, organization of spinal motor neuronal pools and descending pathways to the spinal cord in teleosts will be reviewed, comparing with those in mammals. Special attention is paid to the rubrospinal tract, since the homologue of nucleus ruber (red nucleus: the origin of rubrospinal tract) has remained uncertain in teleosts, until recent.

### *Topographic distribution of spinal motor neurons*

It is well known that different motor neuron pools are distributed topographically within the spinal ventral horn of mammals (Steward, 2000). Motor neurons innervating trunk and cervical muscles occupy medial zone of the ventral horn, while those innervating limb muscles are present laterally (Fig. 1A). Similarly, motor neurons innervating the trunk muscles are present dorsomedially, while motor neurons innervating fin muscles are located ventrolaterally within the ventral horn in teleosts (Finger & Kalil, 1985; Schneider & Sulner, 2006; Fig. 1B). In mammals, descending pathways to the spinal cord may be grouped into medial descending pathways that course through the ventral funiculus and terminate in the ventromedial segment of spinal grey to regulate mainly the motor neurons supplying trunk and cervical muscles and lateral descending pathways that course through the lateral funiculus and terminate in the ventrolateral segment to control mainly the motor neurons innervating limb muscles.

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Another topographic distribution is known in mammals. Motor neurons innervating flexor muscles are present dorsally, while those innervating extensors distribute ventrally within the ventral horn (Fig. 1A). Such topography has not been reported in teleosts so far as we are aware of.

#### *Descending pathways from rhombencephalon*

In mammals, descending pathways from the rhombencephalon to the spinal cord are medial descending pathways that control mainly trunk and cervical muscles.

Vestibular nuclei give rise to descending fibers that are cumulatively called the vestibulospinal tract (Martin, 2003; Fig. 2A). This descending pathway can be further subdivided into lateral and medial components. The former component, lateral vestibulospinal tract, originates from the lateral vestibular nucleus (Deiters' nucleus) and projects to the ipsilateral spinal cord. The latter originates from other vestibular nuclei (mainly medial vestibular nucleus) and terminates in the spinal cord bilaterally. It should be noted that the lateral vestibular nucleus is composed of large neurons and receives fibers from Purkinje cells of the cerebellum.

Rhombencephalic nuclei that correspond to vestibular nuclei of mammals are present in teleosts. Different terminology has been adopted for these nuclei in different species (octaval nuclei, vestibular nuclei, or octavolateral nuclei), and we follow the terminology of McCormick and Braford (1994) in the present report. The anterior, magnocellular, descending, and tangential octaval nuclei receive vestibular input through the octaval (eighth) nerve (McCormick & Braford, 1994), and hence they are called "octaval" nuclei. All of these octaval nuclei have been reported as the origin of spinal descending projections at least in some species studied (Oka *et al.* 1986; Prasada Rao *et al.* 1987; Behrend & Donicht, 1990; Becker *et al.* 1997; New *et al.* 1998; Bosch & Roberts, 2001; Fig. 2B). Among these nuclei, the magnocellular octaval nucleus has been consistently identified as a spinopetal nucleus. Zebrin-II positive fibers from Purkinje cells have been reported to terminate in octaval nuclei including the magnocellular nucleus

(Brochu *et al.* 1990), which is reminiscent of Purkinje cell projections to the lateral vestibular nucleus in mammals. Terminal zones of octavospinal fibers within the spinal grey remain to be determined precisely in teleosts.

Similarly to the vestibulospinal tract in mammals, however, descending pathways from the octaval nuclei in teleosts probably serves motor control depending on the sense of balance, since they receive primary afferents from vestibular organs. It should be noted that lateral line information may also influence the octavospinal pathways, because octavospinal neurons in the magnocellular octaval nucleus extend a dorsally oriented dendrite into the nucleus medialis of rhombencephalic octavolateral area, a primary lateral line center (Yamamoto, unpubl. data in goldfish).

In mammals the reticular formation sends descending fibers to the ventromedial segment of the spinal grey to maintain postures and walking unconsciously (Fig. 2A). Reticulospinal neurons are present in the pons and medulla oblongata with an additional minor population in the mesencephalic tegmentum (Martin, 2003). Reticulospinal neurons are also present in teleosts (Oka *et al.* 1986; Prasada Rao *et al.* 1987; Behrend & Donicht, 1990; New *et al.* 1998; Bosch & Roberts, 2001), which are distributed from the caudal mesencephalic tegmentum to the medulla oblongata (Fig. 2B).

Rhombencephalic reticulospinal neurons in teleosts show clear segmental distribution, and individual neurons are identifiable and can be categorized into several morphological types (Lee & Eaton, 1991; Lee *et al.* 1993).

The Mauthner cell is a gigantic rhombencephalic neurons present in most species of fish and in some **urodele and anuran amphibians (Will, 1991)**. The Mauthner cell is regarded as a specialized component of reticulospinal neurons (Lee & Eaton, 1991; Lee *et al.* 1993; Fig. 2B). Unlike other reticulospinal neurons, the function of Mauthner cell (induction of rapid escape response) is precisely known (Kimmel *et al.* 1980). Reticulospinal neurons that are similar to Mauthner cells and present in other segment probably serve escape responses together with the Mauthner cells (Kimmel *et al.* 1980).

*Descending pathways from mesencephalon*

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In mammals, the superior colliculus projects fibers mainly to the contralateral spinal cord (Martin, 2003; Fig. 2A). The superior colliculus is also called the optic tectum, and hence this pathway is usually called the tectospinal tract. The tectospinal tract is a medial descending pathway and terminates in the ventromedial segment of spinal grey, restricted mainly in the cervical cord. The superior colliculus serves oculomotor control, and the tectospinal tract is involved in controlling movement of the head, coordinated with the eye movement. In teleosts, the optic tectum gives rise to descending fibers. These fibers, however, do not reach the spinal cord but end in the caudal medulla oblongata (Fig. 2B), and are called the tectobulbar tract (Luiten, 1981). A population of the tectobulbar fibers crosses the midline, while the other fibers do not, which is different from tectospinal fibers in mammals. These differences in the descending pathways from the optic tectum may reflect the lack of the neck in teleosts. It should be noted that the tectobulbar fibers may form synaptic contact with reticulospinal neurons and hence might give influences on spinal motor systems indirectly. **The Mauthner cell receives tectal projections (Zottoli *et al.* 1987).**

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The interstitial nucleus of Cajal is a tegmental nucleus that is present rostral to the oculomotor nucleus in mammals. This nucleus receives fibers from the optic tectum, pretectum, and vestibular nuclei, and projects to the oculomotor nucleus, trochlear nucleus, medial vestibular nucleus, and ventromedial segment of the spinal grey (Nieuwenhuys *et al.* 1988). The pathway reaching the spinal cord is a medial descending pathway that is called the interstitiospinal tract (Fig. 2A)). The interstitiospinal tract serves coordination of neck/trunk and eye movements. In teleosts, a spinopetal nucleus is also present rostral to the oculomotor nucleus. This nucleus, called the nucleus of medial longitudinal fascicle, may be homologous to the interstitial nucleus of Cajal, judging from the position and spinal projection (Oka *et al.* 1986). This nucleus sends fibers throughout the length of the spinal cord (Bosch & Roberts, 2001), although the exact sites of terminations within the spinal grey remain unclear. Brain lesion, electrophysiological, and electrical stimulation studies indicate that this nucleus is involved in swimming through the control of trunk and tail muscles (Uematsu & Todo,

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5 1997; Baba *et al.* 2003; Kobayashi *et al.* 2009). A thorough knowledge on the  
6 afferent and efferent connections of the nucleus of medial longitudinal  
7 fascicle would help determine if the nucleus serves similar roles as those of  
8 the interstitial nucleus of Cajal of mammals.  
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12 The nucleus ruber or red nucleus is present in the mesencephalic  
13 tegmentum of mammals. The nucleus ruber is composed of magonocellular  
14 and parvocellular divisions, and the former component gives rise to one of  
15 the two lateral descending pathways to the spinal cord in mammals (Fig. 2A).  
16 The rubrospinal tract crosses the midline and descends through the lateral  
17 funiculus and terminates in the ventrolateral segment of the spinal grey  
18 (Martin, 2003). The rubrospinal tract in involved in the motor control of  
19 limbs. In humans the magnocellular division is poorly developed, and the  
20 rubrospinal tract does not appear to reach lumbar enlargement (Martin,  
21 2003).  
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29 In teleosts the homologue of magnocellular division of nucleus ruber  
30 remained uncertain until recent. Goldstein (1905) identified a “nucleus ruber”  
31 in the midbrain tegmentum of carp, ventrolaterally to the nucleus of medial  
32 longitudinal fasciculus. We call this nucleus the “nucleus ruber of Goldstein”  
33 (NRg) in the present report. Later on, Nieuwenhuys and Pouwels (1983)  
34 identified a “nucleus ruber” in the midbrain tegmentum of rainbow trout,  
35 ventrolaterally to the oculomotor nucleus (nucleus ruber of Nieuwenhuys &  
36 Pouwels, 1983; NRnp), i.e. at a level slightly caudal to that of the NRg.  
37 Subsequent studies indicated that the NRg projects to the contralateral  
38 spinal cord (goldfish; Prasada Rao *et al.* 1987) and the NRnp to the  
39 ipsilateral cord (himé salmon; Oka *et al.* 1986). Differences in the location of  
40 the nuclei and laterality of spinal projections suggest that they are different  
41 nuclei, although both are called “nucleus ruber”. The contralateral spinal  
42 projection of the NRg may support the homology of the NRg with the nucleus  
43 ruber of mammals. It is uncertain, however, whether laterality alone  
44 provides a solid basis to assess the homology. Making the situation further  
45 complex, the two nuclei have not been simultaneously identified in a single  
46 teleost species in a number of subsequent studies (see literatures cited in  
47 Nakayama *et al.* 2016). Therefore, the NRnp might perhaps be the rubral  
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homologue with derived characters (more caudal location and projections to the ipsilateral spinal cord). Analyses on the phylogenetic distribution of the NRg and NRnp in 36 species of actinopterygians by cytoarchitectonic and tract-tracing studies indicated that the NRnp is present only in euteleosts (*sensu* Nelson, 2006) and clupeomorphs and the NRg is present in all species investigated (Nakayama *et al.* 2016)(Fig. 3). Therefore, the NRg is quite likely homologous to the nucleus ruber of mammals. Whether or not the rubrospinal tract serves motor control of pectoral and ventral fins, or homologues of limbs (Yano & Tamura, 2013), remains to be investigated. The NRnp appears to be a derived character in euteleosts and clupeomorphs, as judged from its phylogenetic distribution. Afferent and efferent connections of the NRnp should be studied to understand the functions of the NRnp.

#### *Descending pathways from telencephalon*

In mammals the motor cortex sends out long descending projections to the spinal cord (Martin, 2003; Fig. 2A). The projections can be categorized into lateral and medial corticospinal tracts. The lateral corticospinal tract decussates through the pyramid at the spinomedullary junction, and is also called the pyramidal tract. The lateral corticospinal tract is a lateral descending pathway that courses through the lateral funiculus and terminates in the ventrolateral segment of spinal grey to control mainly limb muscles. The medial corticospinal tract is a medial descending pathway that terminate in the ventromedial segment of spinal grey and serves mainly the control of trunk muscles.

The dorsal telencephalic area or the pallial homologue in teleosts does not appear to project to the spinal cord; a number of tract-tracing studies of the spinal cord have never resulted in labeled cells in the dorsal telencephalic area. This does not mean that the dorsal telencephalic area has nothing to do with the motor control. Electric stimulations of the central part of dorsal telencephalic area elicited nestbuilding behavior in bluegill (Demski & Knigge, 1971). The dorsal telencephalic area probably exerts influences on behavior via descending projections to more caudal brain

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5 regions such as the optic tectum (Murakami *et al.* 1983), NRg (Yamamoto,  
6 unpubl. data in carp), and reticular formation (Luque *et al.* 2008).  
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### 10 **Concluding remarks**

11 Most of the descending pathways from the brainstem to the spinal  
12 cord in teleosts appear to be homologous to those found in mammals,  
13 including the rubrospinal tract that was just recently identified precisely in  
14 teleosts (Fig. 2). **This suggests that the organization of supraspinal centers**  
15 **that drive various motor activities is basically the same in teleosts and**  
16 **mammals. Along the same line, it should be pointed here that dopaminergic**  
17 **diencephalospinal projections, which exerts modulatory influences on the**  
18 **spinal cord (e.g. switch of motor pattern), is also present in teleosts and**  
19 **mammals (Kastenhuber *et al.* 2010; Lambert *et al.* 2012; Björklund &**  
20 **Skagerberg, 1979).**  
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28 Topographical relationship of motoneuron pools for trunk and fin  
29 muscles is similar to that seen for the trunk and limb motorneuron pools of  
30 mammals. Therefore, descending projections to the spinal cord in teleosts  
31 may also be composed of lateral and medial descending pathways as in  
32 mammals, although much remains to be investigated further. It should be  
33 noted that brainstem projections to the spinal cord are similarly organized in  
34 vertebrates, with the exception of cyclostomes that lack an identifiable  
35 rubrospinal pathway and paired fins (Nieuwenhuys *et al.* 1998). The  
36 descending pathway to the spinal cord, which originates from the NRnp in  
37 some teleosts, may be a derived character specific to these fishes.  
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44 The most conspicuous difference in the organization of descending  
45 pathways is the lack of a homologue of corticospinal tract in teleosts. It  
46 should be noted that a homologue of corticospinal tract has not been  
47 identified definitively in other non-mammalian vertebrates (Nieuwenhuys *et*  
48 *al.* 1998). Direct control of the spinal motor system may be a derived feature  
49 that evolved in mammals.  
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## Figure Legend

Figure 1. Topography of motoneuronal pools in the spinal cord of mammals (A) and teleosts (B).

Figure 2. Descending pathways to the spinal cord in mammals (A) and teleosts (B). F: nucleus of medial longitudinal fasciculus; I: interstitial nucleus of Cajal; M: Mauthner cell; MC: motor cortex; ME: mesencephalon; NR: nucleus ruber; NRg: nucleus ruber of Goldstein (1905); NRnp: nucleus ruber of Nieuwenhuys and Pouwels (1983); O: octaval nuclei; R: reticular formation; RO: Rhombencephalon; SP: spinal cord; T: optic tectum (or superior colliculus in mammals); TE: telencephalon; V: vestibular nuclei.

Figure 3. Phylogenetic distribution of nucleus ruber of Goldstein (1905) (NRg) and nucleus ruber of Nieuwenhuys and Pouwels (1983) (NRnp) in actinoptertgians. Double circles indicate the presence of the nucleus as investigated by tract-tracing studies and cytoarchitectonic studies with stained sections. Single circles indicate the presence of the nucleus as investigated by cytoarchitectonic studies with stained sections. Crosses indicate that the nucleus was not identified.

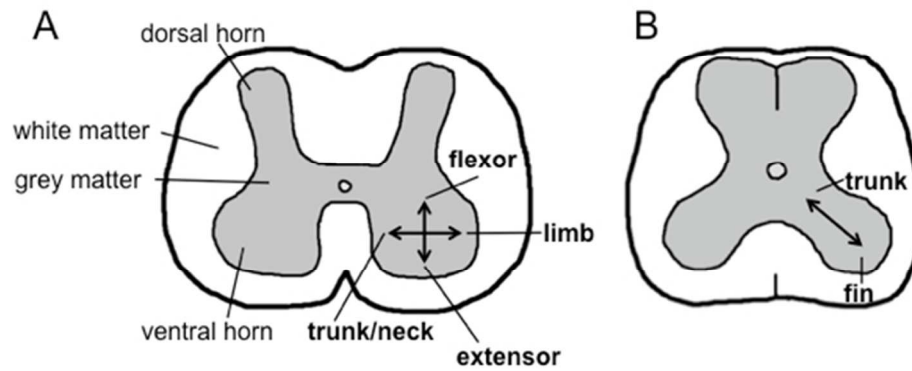


Figure 1. Topography of motoneuronal pools in the spinal cord of mammals (A) and teleosts (B).

225x169mm (72 x 72 DPI)

review

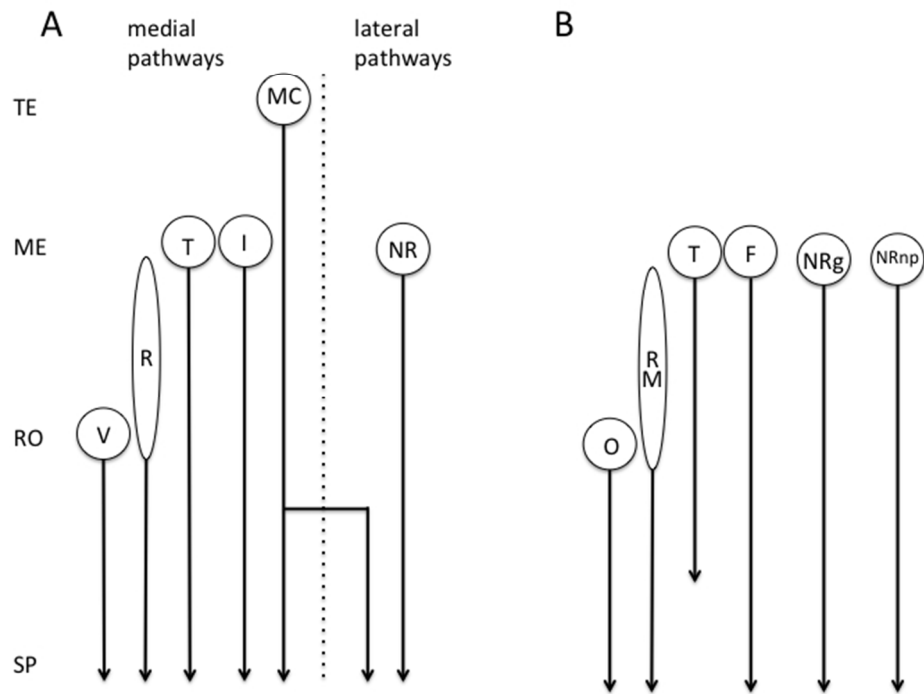


Figure 2. Descending pathways to the spinal cord in mammals (A) and teleosts (B). F: nucleus of medial longitudinal fasciculus; I: interstitial nucleus of Cajal; M: Mauthner cell; MC: motor cortex; ME: mesencephalon; NR: nucleus ruber; NRg: nucleus ruber of Goldstein (1905); NRnp: nucleus ruber of Nieuwenhuys and Pouwels (1983); O: octaval nuclei; R: reticular formation; RO: Rhombencephalon; SP: spinal cord; T: optic tectum (or superior colliculus in mammals); TE: telencephalon; V: vestibular nuclei.

254x190mm (72 x 72 DPI)



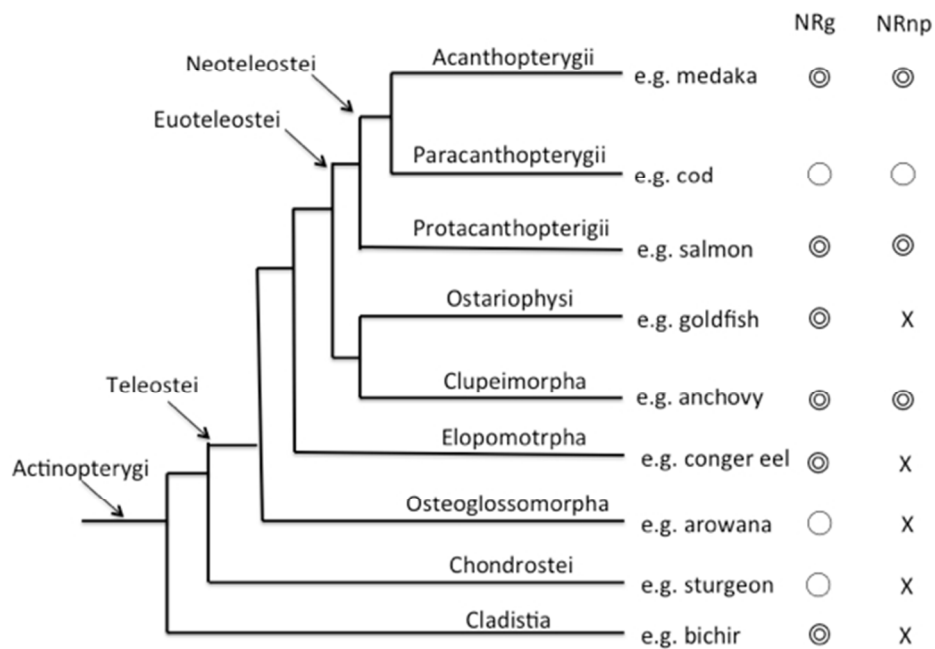


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225x169mm (72 x 72 DPI)