available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research Report

Descending projections to the hindbrain and spinal cord in the paddlefish *Polyodon spathula*

Michael G. Metzen[b], *Mwaka Chambwa*[a], *Lon A. Wilkens*[a], *Michael H. Hofmann*[a,b,*]

[a]*Center for Neurodynamics, Department of Biology, University of Missouri, St Louis, MO 63121, USA*
[b]*Institute for Zoology, University of Bonn, 53115 Bonn, Germany*

ARTICLE INFO

Article history:
Accepted 22 December 2009
Available online 4 January 2010

Keywords:
Descending projections
Hindbrain
Spinal cord
Paddlefish
Midbrain

ABSTRACT

In vertebrates, almost all motor neurons innervating skeletal muscles are located in the hindbrain and spinal cord, and all brain centers that control behavior have descending projections into these parts of the central nervous system. With tracer injections into the spinal cord and hindbrain, we have studied cell groups with descending projections in the paddlefish. Spinal cord injections reveal retrogradely labeled cells in all reticular and raphe nuclei, as well as the nucleus of the medial longitudinal fascicle. Additional cell groups with projections to the spinal cord are the nucleus of the fasciculus solitarius, descending trigeminal nucleus, several octavolateral nuclei, the dorsal hypothalamic nucleus, and the pretectum. The only primary sensory fibers with descending projections are trigeminal fibers. Hindbrain injections reveal a number of additional cell groups in di- and mesencephalon. The most prominent source is the mesencephalic tectum. Other descending cells were found in the dorsal posterior thalamic nucleus, ventral thalamus, torus semicircularis, lateral mesencephalic nucleus, and the central gray of the mesencephalon. Our data show that descending spinal projections are comparable to those of other vertebrates and that the tectum is the most important motor control center projecting to the hindbrain. A surprising result was that the dorsal posterior thalamic nucleus also projects to the hindbrain. This nucleus is thought to be a center that relays

* *Corresponding author*. University of Bonn, Institute for Zoology, Poppelsdorfer Schoss, 53115 Bonn, Germany.
E-mail address: mhofmann@uni-bonn.de (M.H. Hofmann).

Abbreviations: aur, auricles; BDA, biotinylated dextran amine; bo, bulbus olfactorius; cer, cerebellum; cpth, central posterior thalamic nucleus; DAB, diaminobenzidine; don, dorsal octavolateral nucleus; dpth, dorsal posterior thalamic nucleus; fr, fasciculus retroflexus; gcm, griseum centrale mesencephali; lmn, lateral mesencephalic nucleus; Mth, Mauthner cell; mIII, oculomotor nucleus; mes, mesencephalon; meV, nucleus mesencephalicus nervi trigemini; mon, medial octavolateral nucleus; nI, olfactory nerve; nII, optic nerve; nIII, oculomotor nerve; nIV, abducens nerve; nIX, glossopharyngeal nerve; nV, trigeminal nerve; nVII, facial nerve; nVIII, octaval nerv; nLLa, anterior lateral line nerve; nLLp, posterior lateral line nerve; npe, nucleus preeminentialis; nuflm, nucleus of the fasciculus longitudinalis medialis; nufs, nucleus fasciculus solitarius; nX, vagal nerve; oli, inferior olive; PB, phosphate buffer; pd, dorsal periventricular hypothalamus; pl, lateral periventricular hypothalamus; pp, preoptic nucleus; pt, posterior tuberal nucleus; pv, ventral periventricular hypothalamus; prtc, central pretectal nucleus; prtp, periventricular pretectum; rai, raphe inferior; ram, raphe medialis; ri, nucleus reticularis inferior; rm, nucleus reticularis medius; rs, nucleus reticularis superior; sac, stratum album centrale; sc, spinal cord; sch, nucleus suprachiasmaticus; sco, supracommissural organ; sfgs, stratum fibrosum et griseum superficiale; sgc, stratum griseum centrale; sm, stratum marginale; so, stratum opticum; spv, stratum periventriculare; tel, telencephalon; tl, torus longitudinalis; tla, torus lateralis; tm, mesencephalic tectum; ts, torus semicircularis; Vd, nucleus descendens trigemini; vem, magnocellular vestibular nucleus; VIIId, descending octaval nucleus; visc, nucleus visceralis secundarius; Vm, trigeminal motor nucleus; vmth, nucleus ventromedialis thalami; Xm, vagal motor nucleus

0006-8993/$ – see front matter
doi:10.1016/j.brainres.2009.12.078

sensory information to the telencephalon. Further studies are needed to determine the complete set of projections of the dorsal thalamus in paddlefish and other fishes to gain insights into its functional role.

1. Introduction

The aim of this study was to identify the major neuronal tracts that send descending axons to the spinal cord and hindbrain in the paddlefish (*Polyodon spathula*), a sister group to the sturgeons representing a more basal group of actinopterygian fishes. The actinopterygian radiation of ray-finned fishes consists of five major groups: Cladistia, which are reedfishes and the most basal group; Chodrostei, which are the sturgeons and paddlefishes; Ginglimodi, the gars; Halecomorphi, of which only the bowfin Amia is extant; and the large radiation of Teleostei, the bony fishes. The teleosts consist of four major groups, of which the largest is the Euteleostei, and that group includes a number of the species discussed herein, such as the ostariophysans (goldfishes, carp, and catfishes), trout, and the very large radiation of percomorph fishes that includes perciforms (Nelson, 2006).

Cell groups with descending connections to the spinal cord are the sole source of neurons that can modulate or initiate trunk movements, since all the motor neurons innervating trunk muscles are located in the spinal cord (Landmesser, 1980; Westerfield et al., 1986). Motor neurons innervating cranial muscles are all located in the rhombencephalon (Nieuwenhuys et al., 1982), with the exception of the oculomotor nucleus that innervates eye muscles (Butler and Hodos, 2005). Much of the motor control is organized within the spinal cord or hindbrain, but forebrain and midbrain centers that modulate behavior must ultimately send fibers to the hindbrain.

Olfactory and visual information enters the forebrain, and most information from the electrosensory, the mechanosensory lateral line, and the auditory system is relayed to the midbrain. To understand information processing in these modalities and identify the major pathways that transform sensory information into motor activity, it is important to get an overview of all pathways descending to motor centers in the hindbrain and spinal cord. Descending afferents of the spinal cord are well investigated in a number of species (Corvaja and d'Ascanio, 1981; d'Ascanio and Corvaja, 1981; Prasada Rao et al., 1987, Prasada Rao et al., 1993; ten Donkelaar, 1976, 1982), but there are currently no studies that describe the complete set of cell groups with descending projections to the hindbrain. Many studies are focused on tectal efferents, which constitute probably the most prominent descending pathway, but little is known about additional sources.

In this study, we investigated descending pathways in the paddlefish as part of a larger project to understand the basic functional organization of the fish brain. Paddlefish, like sturgeons, have a relatively simple brain organization that is similar to that in bichirs, reedfish, and garfish. Hagfish, lampreys, elasmobranchs, and teleosts have different specializations with many features that are probably highly derived and therefore do not represent the ancestral condition. The paddlefish brain, on the other hand, may provide us with information on how major descending pathways are organized in a brain that probably has not changed much in over 100 million years following the appearance of fossils in the family Polyodontidae (Grande et al., 2002).

2. Results

2.1. Spinal cord injections

In eight animals, tracer injections were made into the spinal cord at a level just caudal to the large hematopoietic organ situated on top of the spinal cord. Fig. 1 shows a dorsal view of the brain of the paddlefish and the level of the sections for the following figures. We adopted the nomenclature of Nieuwenhuys et al. (1998).

Depending on the exact location of the injection site, various cell groups were retrogradely labeled. The results of a combination of all eight cases are shown in Fig. 2. Most of the cells were located in the hindbrain. Within the hindbrain, the most caudally located cell group is the nucleus descendens of the trigeminus (Vd), which is labeled bilaterally (Figs. 2A and 3A) just anterior to the obex. At the more rostral level of this nucleus, some cells of the inferior reticular nucleus (ri) were

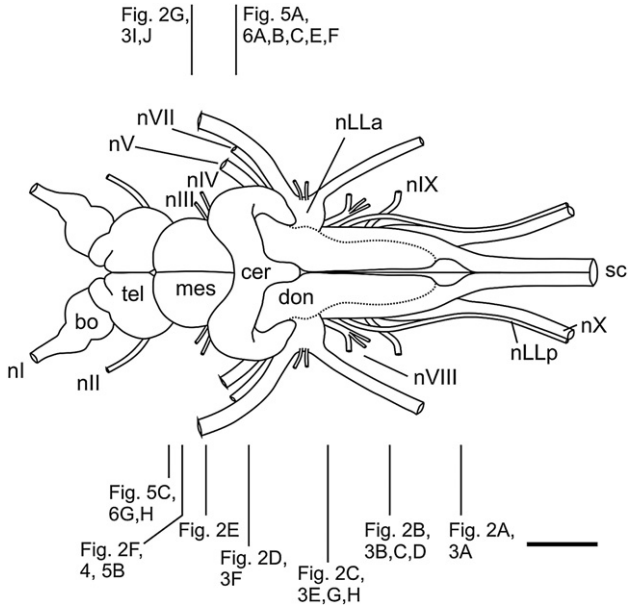

Fig. 1 – Dorsal view of the brain with cranial nerves of *Polyodon spathula*. The dashes indicate the location of cross sections shown in the following figures. Scale bar=3 mm (modified after Pothmann et al. (2009)).