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Research Report

Distribution of somatostatin immunoreactive neurons and fibres in the central nervous system of a chondrostean, the Siberian sturgeon (*Acipenser baeri*)

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A R T I C L E   I N F O

A B S T R A C T

Somatostatin (SOM) is a neuropeptide that is widely distributed in the central nervous system of vertebrates. Two isoforms of somatostatin (SS1 and SS2) have been characterized in sturgeon and *in situ* hybridisation studies in the sturgeon brain have demonstrated that mRNAs of the two somatostatin precursors (PSS1 and PSS2) are differentially expressed in neurons [Trabucchi, M., Tostivint, H., Lihrmann, I., Sollars, C., Vallarino, M., Dores, R.M., Vaudry, H., 2002. Polygenic expression of somatostatin in the sturgeon *Acipenser transmontanus*: molecular cloning and distribution of the mRNAs encoding two somatostatin precursors. J. Comp. Neurol. 443, 332–345.]. However, neither the morphology of somatostatinergic neurons nor the patterns of innervation have yet been characterized. To gain further insight into the evolution of this system in primitive bony fishes, we studied the distribution of somatostatin-immunoreactive (SOM-ir) cells and fibres in the brain of the Siberian sturgeon (*Acipenser baeri*). Most SOM-ir cells were found in the preoptic area and hypothalamus and abundant SOM-ir fibres coursed along the hypothalamic floor towards the median eminence, suggesting a hypophysiotrophic role for SOM in sturgeon. In addition, SOM-ir cells and fibres were observed in extrahypothalamic regions such as the telencephalon thalamus, rhombencephalon and spinal cord, which also suggests neuromodulatory and/or neurotransmitter functions for this peptide. Overall there was a

Abbreviations: AC, anterior commissure; AP, area postrema; AU, auricula cerebelli; CB, corpus cerebelli; CC, central canal; cg, central grey; CP, choroid plexus; Dc, central part of the dorsal telencephalon; Dd+Dl, dorsal and lateral parts of the dorsal telencephalon; Dm, dorsomedial part of the dorsal telencephalon; Dp, posterior part of the dorsal telencephalon; FR, fasciculus retroflexus; H, habenula; HL, hypothalamic lobes; i, infundibulum; III, third ventricle; IIIn, oculomotor nucleus; Ip, interpeduncular nucleus; IV, fourth ventricle; IVn, trochlear nucleus; IXm, glossopharyngeal motor nucleus; IXr, glossopharyngeal motor root; LR, lateral hypothalamic recess; ME, median eminence; MLF, medial longitudinal fascicle; MO, medulla oblongata; NAT, anterior tuberal nucleus; NDT, dorsolateral thalamic nucleus; NIL, neurointermediate lobe of the neurohypophysis; NLT, lateral tuberal nucleus; NPOp, parvocellular preoptic nucleus; NRP, posterior recess nucleus; OB, olfactory bulb; OCh, optic chiasm; OT, optic tectum; OVLT, vascular organ of the terminal lamina; P, pineal organ; PC, posterior commissure; PD, pars distalis of the hypophysis; Pi, pituitary; POR, posterior recess; PR, preoptic recess; PT, posterior tubercle; Rad, dorsal raphe nucleus; Ras, superior raphe nucleus; Ri, inferior reticular formation; Rs, superior reticular formation; SC, spinal cord; SGN, secondary gustatory nucleus; SGT, secondary gustatory tract; SV, saccus vasculosus; T, telencephalon; TG, mesencephalic tegmentum; tv, telencephalic ventricle; VC, valvula cerebelli; Vd, dorsal part of the ventral telencephalon; Vl, ventrolateral nucleus of the ventral telencephalon; VM, ventromedial thalamic nucleus; Vv, ventral part of the ventral telencephalon; Xm, vagal motor nucleus; Xr, vagal motor root; Xv, vagal lobe

good correlation between the distribution of SOM-ir neurons throughout the brain of *A. baeri* and that of PSS1 mRNA in *Acipenser transmontanus*. Comparative analysis of the results with those obtained in other groups of fishes and tetrapods indicates that widespread distribution of this peptide in the brain is shared by early vertebrate lines and that the general organization of the somatostatinergic systems has been well-conserved during evolution.

1.   Introduction

Somatostatin (SOM) is a neuropeptide originally isolated from the ovine hypothalamus because of its ability to inhibit growth hormone secretion (Brazeau et al., 1973). Two major forms of SOM are produced by tissue-dependent processing of the same precursor protein (Patzelt et al., 1980; Schindler et al., 1996). One consists of 14 amino acids (cyclic tetradecapeptide SOM-14), and the other has an N-terminal extension (SOM-28) (Bohlen et al., 1980). The primary structure of SOM-14 has been strongly conserved during evolution, although different molecular forms with similar biological activity have been found (Tostivint et al., 2004). Two isoforms of SOM-14 have been identified in sturgeons: one known as SS1, which is identical to mammalian S14, was isolated from the gastrointestinal tract of the pallid sturgeon *Scaphirhynchus albus* (Kim et al., 2000), and the other one known as SS2, which is a variant with one amino acid changed ([Pro^2] S14), was isolated from the pituitary of the Russian sturgeon *Acipenser gueldenstaedti* (Nishii et al., 1995). Moreover, two SOM precursors, which are encoded by two distinct genes, have been characterized in sturgeons: one precursor (PSS1) generates SOM-14 and the other one (PSS2) gives rise to the [Pro^2] SOM-14 variant (Trabucchi et al., 2002). *In situ* hybridisation studies have demonstrated that mRNAs of the two SOM precursors (PSS1 and PSS2) are widely but differentially expressed in numerous regions of the brain of the white sturgeon (*Acipenser transmontanus*) (Trabucchi et al., 2002). However, neither the morphology of somatostatinergic neurons nor the patterns of innervation have yet been characterized in chondrosteans (sturgeons and paddlefishes), considering the most primitive extant ray-finned bony fishes (Actinopterygians) (Nieuwenhuys, 1998).

Numerous immunohistochemical studies have demonstrated the wide distribution of SOM in the central nervous system of many vertebrate taxa, including mammals (Elde and Parsons, 1975; Beal et al., 1983; Johansson et al., 1984; Vincent et al., 1985; Cotter and Laemle, 1987; Shimada and Ishikawa, 1989; Desjardins and Parent, 1992), birds (Shiosaka et al., 1981; Takatsuki et al., 1981), reptiles (Fasolo and Gaudino, 1982; Bear and Ebner, 1983; Weindl et al., 1984; Alponti et al., 2006), amphibians (Vandesande and Dierickx, 1980; Inagaki et al., 1981; Laquerrière et al., 1989; Petkó and Orosz, 1996; Vallarino et al., 1998, 2006; González et al., 2003; Mathieu et al., 2004; López et al., 2007) and some fishes (*agnathans*: Nozaki and Gorbman, 1983; Wright, 1986; Yáñez et al., 1992; *elasmobranchs*: Chiba et al., 1989; Meurling and Rodriguez, 1990; *teleosts*: Kah et al., 1982; Vigh-Teichmann et al., 1983; Olivereau et al., 1984; Grau et al., 1985; Margolis-Nunno et al., 1987; Bonn and Köning, 1989; Batten et al., 1990; Sas and Maler, 1991; Pickavance et al., 1992; Becerra et al., 1995; *dipnoans*: Vallarino et al., 1997).

However, similar studies are lacking in chondrosteans, and for this reason we analysed the distribution of SOM-immunoreactive (SOM-ir) cells and fibres in the central nervous system of the Siberian sturgeon (*Acipenser baeri*). Here we compare our results with those obtained in other vertebrates, especially fishes, to gain further insight into the organization and evolution of somatostatinergic systems.

2.   Results

Numerous SOM-ir cells and fibres were observed in several brain region of the Siberian sturgeon. The terminology used for most structures is adopted from that of Nieuwenhuys (1998). We also used the terminology of Rupp and Northcutt (1998) for the hypothalamus and that of Huesa et al. (2006) for the telencephalon.

The olfactory bulbs lacked SOM-ir cells and only showed very scarce SOM-ir fibres. The most rostral SOM-ir cells were observed in telencephalic hemispheres, in both the pallium and the subpallium. These cells were not grouped into discrete nuclei but scattered throughout the dorsal, lateral and central parts of the dorsal telencephalon (Figs. 1A–D and 2A, B), and also in the ventral telencephalon (Figs. 1A, B and 2C). SOM-ir cells in the dorsal telencephalon (pallium) were generally smaller than those in the ventral telencephalon (subpallium). Most of the subpallial SOM-ir cells were moderately stained medium-sized bipolar neurons, from which thick dendrites extended in adjacent areas, and were observed both in periventricular cell layers and in the lateral area, where abundant cells were located in the ventrolateral nucleus (Fig. 2C). Beaded thin SOM-ir fibres were observed in various telencephalic regions, and the innervation was particularly rich in the dorsal telencephalic area (Figs. 1A–D and 2A), while the ventral telencephalic area showed moderate SOM-ir innervation (Figs. 1A, B and 2A). In the sturgeon dorsal telencephalon, which consists of several regions (medial, dorsal plus lateral, central, posterior: see Huesa et al., (2006)), differences in density of SOM-ir innervation were observed among regions. The dorsal plus lateral part and the posterior region were the most richly innervated. In lesser innervated pallial regions SOM-ir cells were larger than those located in densely innervated pallial regions (Fig. 2B).

In the preoptic area, abundant SOM-ir neurons were found in the parvocellular preoptic nucleus, most in a rich-celled layer bordering the preoptic recess (Figs. 1C, D and 2D), although some of them were separated from the periventricular region (Fig. 2D). The periventricular neurons showed bipolar morphology, with a process that contacted the cerebrospinal fluid (CSF-C cells) and a long ventrolateral process. The preoptic area showed moderate innervation by thin beaded SOM-ir fibres (Figs. 1C, D and 2D). A few SOM-ir cells were also