Forebrain atlas of Japanese jack mackerel *Trachurus japonicus*

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Abstract We have prepared a forebrain atlas of the Japanese jack mackerel, *Trachurus japonicus* (Perciformes: Carangidae) to provide basic knowledge on the brain that regulates various physiological conditions and behavior. The Japanese jack mackerel was selected as a model species of Carangidae, since the brain of this species is relatively small for a member of this family and is thus suitable for the production of a brain atlas. The external morphology of the brain is described, and complete series of transverse sections were prepared and stained by cresyl violet. As observed externally, the optic tectum and cerebellar crest appear to be somewhat hypertrophied in comparison with other brain parts, suggesting importance of visual and lateral line information for this species. The cerebellar corpus is also relatively large, protruding rostrally on top of the optic tectum. This may be related to the requirement of precise motor control for shoaling behavior. A number of sections were selected so that all the forebrain nuclei are demonstrated in a series of figures. Brief anatomical descriptions for each structure were also given in the text. As observed with sections, a major finding in the present study of the Japanese jack mackerel is the presence of as many as seven regions within the lateral part of dorsal telencephalic area. The lateral part of the dorsal telencephalic area is a presumed visual center, and this feature is also in line with the importance of vision for the Japanese jack mackerel.

Keywords Japanese jack mackerel・*Trachurus japonicus*, teleost fish・Forebrain atlas

Introduction

Neurobiological studies of fish are indispensable to understand the neural substrate that determines the behavioral characteristics of each species and to reveal the neural mechanisms that regulate seasonal breeding and gonadal development. Furthermore, in general, fish has to learn various things because they usually experience major habitat shifts during ontogeny, self-protection from predator, and breeding. That is, they face different cognitive challenges during their life history (Masuda and Ziemann 2000). Thus, fish should also possess relatively high cognitive, learning, and memory abilities, whose mechanisms could only be understood more precisely by neurobiological studies.

Knowledge on the cytoarchitecture and nuclear organization of the brain is the basis to perform any neurobiological studies in the species in question, since, for example, studies on the distributions of some neurochemical substances can only be made fruitful based on proper descriptions of brain nuclei. Similarly, neural connections cannot be described and analyzed properly without correct knowledge on brain regions and nuclei. A brain atlas provides such basic knowledge on the cytoarchitecture and nuclear organization of the brain. Since the nuclear organization differs substantially in different groups of fish (Tuge et al. 1968; Ito and Yoshimoto 1991; Ito et al. 2007), brain atlases for major groups of fish are at least necessary to promote comparative neurobiological researches in fish. Morphological features of the peripheral nervous system have been used for considerations on phylogeny of teleosts (Nakae and Sasaki 2007). Comparisons on the brain morphological characters in different species may also shed new light on phylogenetic analyses, and brain atlas of different species would provide data that can be used for such studies as well.

In teleosts, a number of brain atlases have been published so far. A monumental work achieved by Tuge et al. (1968) presents the external brain morphology and brain sections in as

many as 102 species of teleosts in Japan, covering most of the major taxa. However, the terminology adopted in that study (Ariëns Kappers et al. 1936) is old, and many neuroanatomical terms should be corrected based on the current knowledge. Also, the numbers of brain sections presented per species were only 10–14 for most species, and only the major brain regions such as the thalamus were indicated without identifying each nucleus. Detailed brain atlases focusing on single or a few species have been published. Many of such atlases focus on a specific brain part. For example, forebrain (telencephalon and part of diencephalon) atlases of the goldfish *Carassius auratus* (Cypriniformes: Cyprinidae,) and the mummichog *Fundulus heteroclitus* (Cyprinodontiformes: Fundulidae) were reported by Peter and Gill (1975) and Peter et al. (1975), respectively. Telencephalic brain atlases have been published for the channel catfish *Ictalurus punctatus* (Siluriformes: Ictaluridae) (Bass 1981), the banded knife-fish *Gymnotus carapo* (Gymnotiformes: Gymnotidae)(Corrêa et al. 1998), a cichlid *Astatotilapia burtoni* (Perciformes: Cichlidae) (Burmeister et al. 2009), the dwarf snakehead *Channa gachua* (Perciformes: Channidae) (Baile and Patle 2011), and the pebbled butterflyfish *Chaetodon multicinctus* (Perciformes: Chaetodontidae) (Dewan and Tricas 2014). Diencephalic brain atlases have been published for the Atlantic herring *Clupei harengus* (Clupeiformes: Clupeidei) (Butler and Northcutt 1993), the goldfish (Braford and Northcutt 1983), the channel catfish (Striedter 1990), and *Astatotilapia burtoni* (see Fernald and Shelton 1985). However, brain atlases covering throughout the neuraxis are rare. Such brain atlases, which should be most useful for neurobiological studies, have been published for the Japanese eel *Anguilla japonica* (Anguilliformes: Anguillidae) (Mukuda and Ando 2003), the zebrafish *Danio rerio* (Cypriniformes: Cyprinidae) (Wullimann et al. 1996), the brown ghost knife-fish *Apteronotus leptorhynchus* (Gymnotifomes: Apteronidae) (Maler et al. 1991), the medaka *Oryzias latipes* (Beloniformes: Adrianichthydae) (Ishikawa et al. 1999), the turquoise killifish *Nothobranchius furzeri* (Cyprinodontiformes: Nothobranchiidae,) (D'Angelo 2013), and the

European seabass *Dicentrarchus labrax* (Perciformes: Moronidae) (Cerdá-Reverter et al. 2001a, 2001b, 2008). Considering the number of species of actinopterygians, published whole brain atlases are incredibly few. In particular, only a single report (European sea bass) for perciforms is amazing, while this group of fish exhibits enormous diversification (Nelson 2006). In the present study, therefore, we have prepared a brain atlas of the Japanese jack mackerel *Trachurus japonicus* (Perciformes: Carangidae). So far as we are aware of, no complete brain atlas have been reported in this family. The Japanese jack mackerel migrates in school to inshore during the juvenile stage and spawns at the offshore associated with the floating objects such as jellyfish and seaweeds, and thus experiences much changes in habitat (Sassa et al. 2006, 2008). This species inhabits in relatively complex environment, and possibly the brain of the Japanese jack mackerel is complex with good abilities of learning and memory. In fact, studies on the spatial learning of this species have been conducted (Masuda and Ziemann 2000; Takahashi et al. 2010). A relatively small brain size that reflects small body size facilitates the production of the brain atlas in this species.

In the present study, a forebrain atlas of the Japanese jack mackerel is reported, and the atlas from the midbrain to the spinal cord will be reported in the near future. This series of studies are expected to provide a solid basis for neurobiological studies in the Japanese jack mackerel, and also add to comparative biology of teleosts. The brain atlas for the Japanese jack mackerel will be also useful for future studies on other species of carangids from the points of view of comparative biology, including phylogeny (see Santini and Carnevale 2015).

Materials and methods

Five Japanese jack mackerel *Trachurus japonicus* of both sexes, measuring approximately 19.5cm in standard length, were obtained from a commercial source. All experimental procedures described below were under the guidelines of Animal Experiment Committee of Nagoya University, which conform to the official regulations for animal use for scientific research in Japan. Following deep anesthesia with tricaine methane sulfonate (MS222; over 300mg/L; Sigma), the jack mackerel were perfused through the conus arteriosus with 0.9% saline followed by a mixed solution of 2% paraformaldehyde and 1% gultaraldehyde in 0.1M phosphate buffer (PB), pH 7.4. The brains were dissected and postfixed in the fresh solution of the same fixative at 4^{o}C overnight. The brains were immersed in 0.1M PB containing 20% sucrose for one day at 4^{o}C for cryoprotection. The brains were then embedded in 5% agar (Sigma, Type IX: ultra low gelling temperature) containing 20% sucrose, frozen in normal hexane at –60^{o}C, and sectioned transversely at 40μm thick on a cryostat. The sections were mounted on gelatin-coated slides and air-dried for 90min. After washes in 0.1M phosphate-buffered saline, the sections were dehydrated through an ascending series of ethanol to facilitate Nissl staining with cresyl violet. After rehydration through a descending series of ethanol, the sections were stained with 0.05% cresyl violet, dehydrated through an ascending series of ethanol, cleared with xylene, and cover-slipped with Permount (Fisher Scientific). We have mapped all forebrain brain nuclei and demarcated the boundaries between the nuclei by consulting with available literatures that can assist in identifying the brain nuclei. The brain atlas presents photographic figures of brain sections on the right side and corresponding line drawings on the left side. This way of presentation enables simultaneous visualization of the actual sectional images (cytoarchitecture) of brain nuclei and the boundaries between them. The images of sections were taken with a digital camera (DP70; Olympus, Tokyo, Japan) controlled by computer software (CellSens; Olympus) and the outline of sections and nuclear boundaries were sketched using Adobe Photoshop (Adobe, San Jose, CA) and a

graphic tablet (CTE-640, Wacom, Saitama, Japan). Brightness and contrast of the photographs were modified as necessary using Adobe Photoshop. The nomenclature for the brain structure of the Japanese jack mackerel followed previous studies of other fish species such as Peter and Gill (1975), Braford and Northcutt (1983), Ishikawa et al. (1999), Cerdá-Reverter (2001a,b), Yamamoto and Ito (2005, 2008), and Dewan (2014). Other terms were also introduced as necessary, citing the literature.

Results

External brain morphology. Before we go on to the forebrain atlas, the external brain morphology of the Japanese jack mackerel is briefly described (Figs. 1, 2). In the dorsal view, we can clearly see the dorsal aspects of olfactory bulb (OB) and telencephalon (TE) of the forebrain, optic tectum (TO) of the mesencephalon, corpus cerebelli (CC) and cerebellar crest (CrC) of the rhombencephalon, and spinal cord (SC). In the ventral view, we can clearly identify the inferior lobe (LI) of the diencephalon or the lateral part of hypothalamus and the ventral aspect of the SC. The TO is relatively large, and the CrC is very clearly identifiable and spans a considerable rostrocaudal length. The CC is relatively large and protrudes rostrally on top of the TO. The OB of the Japanese jack mackerel is of the sessile type (located immediately rostral to the TE and connected to the olfactory epithelium through a long olfactory nerve), unlike the stalked-type OB (located immediately caudal to the olfactory epithelium, being connected to the TE with a long olfactory tract). We did not note any sex differences in the external brain morphology.

Forebrain atlas. Among the five brains of the Japanese jack mackerel sectioned and stained, an almost perfect series of sections was obtained for a female. The same set of brain

nuclei was identified in both sexes. Sex differences may be present, e.g. in the size of nuclei relative to the whole brain. However, this is beyond the scope of the present analyses. We, therefore, use the best series of sections from that female for presentations of brain sections in the present study. In the following, we will describe the brain nuclei from rostral to caudal. The forebrain, also called the prosencephalon, has traditionally been divided into the TE and diencephalon.

Telencephalon. The TE is comprised of the OB, telencephalon proper (or telencephalic hemisphere), and preoptic area, and is bounded caudally by the diencephalon. The telencephalon proper is further divided into the dorsal and ventral telencephalic areas. The ventricle of the TE in the Japanese jack mackerel is "T"-shaped as in other teleosts, bordered dorsally by the extended roof plate and sandwiched by the right and left hemispheres.

Olfactory bulb.–At the mid-OB level, three layers are clearly recognized: the glomerular layer (GRL), mitral cell layer (ML), and granule cell layer (GCL), in this order from superficial to deep (Fig. 3, section #53). More rostrally, an additional layer is recognized on the external margin of the bulb. This layer is the primary olfactory fiber layer that is composed of olfactory nerve fibers. The latter layer becomes thinner and becomes difficult to identify clearly at more caudal levels of the bulb, since olfactory nerve fibers terminate in glomeruli and becomes reduced in number caudally. The ganglion of terminal nerve (TNggl) is identifiable in the caudalmost region of the bulb (Fig. 3, sections #80 and #86).

Dorsal telencephalic area.–The dorsal telencephalic area or dorsal telencephalon corresponds to the pallium (neocortex, olfactory cortex, hippocampus and cortical amygdala) of mammals (Kage et al. 2004). It occupies the dorsal half of the telencephalic hemisphere and spans the entire rostrocaudal length of the hemisphere. It can be subdivided into several parts: the lateral (Dl), medial (Dm), central (Dc), dorsal (Dd), and posterior (Dp) parts of dorsal telencephalic area, and the nucleus taenia (nT).

The Dl occupies the lateral zone of the dorsal telencephalic area and faces the ventricle dorsolaterally. It extends a considerable rostrocaudal length within the dorsal telencephalic area. The Dl can be subdivided further into multiple regions composed of cells with different size, density, and staining intensity. These Dl regions are termed in a numerical order (Dl1 to the Dl7), according to the sequence of appearances as we observed sections from rostral to caudal (Figs. 3–7). In section #80 (Fig. 3), the rostralmost region of the Dl or Dl1 is clearly identifiable, occupying the lateral half of the dorsal telencephalic area. The Dl1 is composed of small cells and appears somewhat laminar. Medially adjacent to the Dl1 is the rostrolateral region of the Dc (rDcl) that is composed of larger cells than those of Dl1. Caudally, a round structure appears dorsal to the Dl1 (Fig. 3, section #86). This structure corresponds to the rostral margin of Dl2, which soon becomes fused with the Dl1 caudally, indicating its identity as a region of the Dl. Cells in the Dl2 are larger and more diffusely distributed than those in the Dl1. The Dl3 is a small region within the Dl that is composed of very tightly packed cells (Fig. 3, section #86). The Dl3 is replaced by the Dl2 when the latter Dl region becomes contiguous to the Dl1 (Fig. 3, section #96). The Dl1 and Dl2 continue for considerably rostrocaudal distances (Figs. 3–5). Caudally, a new region of Dl (Dl4) appears medial to the Dl1 (Fig. 4, section #103). The Dl4 begins as a narrow dorsoventral band of cells, and a cell-sparse zone separates the Dl4 from the Dl1. Cells in the Dl4 show very dense staining, clearly distinguishing this Dl region from other Dl regions. The Dl4 expands laterally as the section level proceeds caudally. A bit more caudally, a Dl region of lower cell density (Dl5) appears lateral to the Dl4 (Fig. 4, section #116). More caudally, the Dl5 becomes larger replacing the Dl2 dorsally. A cell-sparse zone can be recognized that separates the Dl5 from the Dl2 (Fig. 5). The cell bodies of the Dl4 and Dl5 appear similar in terms of their sizes but the cells in the Dl4 show denser staining than those in the Dl5. The Dl4 disappears at the level of anterior commissure (ac), replaced medially by the Dp. The Dl6 appears as an island of tightly packed

cells dorsal to the Dp (Fig. 5, section #126). The position of this Dl cell group shift ventrolaterally as the section level proceeds caudally (Fig. 5, section #129 and Fig. 6, section # 135). Dorsomedial to the Dl6 appears the last Dl region to be described, or the Dl7, which is composed of less tightly packed cells that are larger than those of the Dl6 (Fig. 6, section #135). Dorsal and ventral cell-sparse zones distinguish the Dl7 from the Dl5 and the Dp, respectively (Fig. 6, section #135–140 and Fig. 7, section # 143).

The Dm occupies the medial zone of the dorsal telencephalic area and faces the telencephalic ventricle medially and dorsally. It can be subdivided into the dorsal (dDm) and ventral (vDm) regions. In general the cells in the dDm are larger, more diffusely distributed, and less intensely stained than those in the vDm. A cell-sparse zone represents the boundary between the regions. The dDm is further subdivided into the dDm1 and dDm2, and the vDm into the vDm1, vDm2, and vDm3 (Figs. 3–7). Although the cell sizes do not vary substantially in different subregions of vDm, clustering, arrangement of cells and cell sparse gaps show distinction of these subregions. Rostrally, the dDm1 is located medial to the rostrolateral region of Dc (rDcl), and a cell-free band separates these dorsal telencephalic regions (Fig. 3, section #80). The dDm1 is replaced by the dDm2 dorsomedially (Fig. 4, section #103). The dDm1 is composed of tightly packed and well-stained cells while cells in the dDm2 appear larger in size and less well stained that are distributed more diffusely. Slightly rostral to the rostral margin of the dDm1, more densely stained cells of the vDm1 appear ventral to the dDm1 (Fig. 3, section #86). The vDm1 extends laterally as the section level goes caudally. More caudally a group of very tightly-packed and densely-stained cells appears ventral to the vDm1 (Fig. 4, section #110). This cell group, or the vDm2, continues slightly caudal to the ac (Fig. 6, section #135), being capped by the vDm1 dorsally. At some levels, a cell sparse gap marks the boundary between these vDm subregions (Fig. 4, section #116). Caudal to the ac, a new, less densely stained cell group (vDm3) emerges dorsal to the

vDm1 (Figs.5, 6). It should be also noted that right and left vDm fuse at levels caudal to the ac (Figs. 5, 6).

The Dc occupies the central zone of the dorsal telencephalic area, as the name implies. In general, component cells of this part are large. Rostrally, it is located between the Dm and Dl, where the rostral region of Dc (rDc) is recognized. Two groups of cells can be recognized in the rDc; the medial (rDcm) and lateral (rDcl) subregions (Fig. 3). More caudally, only a single population of cells, or the Dc proper, is recognized (Fig. 3, section #96). Component cells of the Dc are larger and more diffusely distributed than those in the rostral Dc. The Dc is bordered dorsally by the dDm and Dd which will be described below in more detail, medially by the vDm, and laterally by the Dl (Figs. 3–7).

The Dd appears a bit caudal to the rostral margin of the Dl2 (Fig. 3, section #96). This part contains very tightly packed and well-stained cells. It is present lateral to the dDm, medial to the Dl, and dorsal to the Dc (Figs. 3–6). Cells in the rostral zone of the Dd are small. At the level of the ac (Fig. 5, section #126), larger cells appear in the ventral zone of the Dd, which is referred to as the magnocellular region of Dd (Ddmg; Figs. 5, 6) after Giassi et al. (2012). In the dorsal zone of caudal Dd, small cells are still present, which are caudal continuation of the small cell population of the Dd that emerged more rostrally. Further caudally, the Dd disappears and the region between the Dm and Dl is occupied by the Dc (Figs. 6, 7).

The rostral margin of the Dp appears roughly at the level of the ac, replacing the Dl4 (Fig. 5). It is located in the caudolateral zone of the dorsal telencephalic area and is bounded dorsally by the Dl5, Dl6 and Dl7 in this sequence rostrocaudally and by the preoptic area medially (Figs. 5–7). A shallow sulcus separates the Dp from the Dl (Dl6 and Dl7).

The nT is a small nucleus that is clearly recognizable near the caudal end of the dorsal telencephalic area, ventromedially adjacent to the Dp (Fig. 7, section #143). The nT is composed of small, round, well-stained, and densely packed cells.

Ventral telencephalic area.–The ventral telencephalic area or the ventral telencephalon is present below the dorsal telencephalic area and is further divided into several parts: the lateral (Vl), dorsal (Vd), ventral (Vv), supracommissural (Vs), intermediate (Vi), and postcommissural (Vp) parts of the ventral telencephalic area, and the entopeduncular nucleus (E).

TheVl is situated in the lateral part of the ventral telencephalic area and is medial to the Dl (Figs. 3, 4). This ventral telencephalic part is small, dorsoventrally elongate, and its component cells are round and loosely distributed. They are slightly larger and less densely stained than those in the other ventral telencephalic parts.

The Vd is identifiable in the dorsalmost aspect of the ventral telencephalon, lying along the telencephalic ventricle. Rostrally, it emerges above the ganglion of terminal nerve at the transitional zone between the olfactory bulb and the telencephalic hemisphere. A bit more caudally, it is bordered dorsally by the vDm and Dc (Figs. 3–7). Cell bodies of the Vd neurons are small, round, densely packed, and well-stained with cresyl violet. A cell-sparse zone marks the boundary with the Vv.

The Vv is present ventral to the Vd and faces the telencephalic ventricle. The Vv appears a bit caudal to the rostral margin of the Vd (Fig. 3, section #96). The cell bodies of Vv neurons are smaller than those in the Vd, but they are also densely distributed, round and well-stained with cresyl violet.

The Vs appears caudal to the Vv and dorsally adjacent to the ac (Fig. 5). The component cells appear a bit smaller than those in the Vv and are well-stained with cresyl violet.

The Vp replaces the Vs caudally (Fig. 5, section #140; Fig. 6, section #143). The cell bodies of Vp are small and loosely distributed in comparison with those of Vd and Vv. They are not well-stained with cresyl violet.

The Vi is laterally adjacent to the Vp (Fig. 6, section #140) and might perhaps be regarded as the lateral extension of the Vp. However, the two ventral telencephalic parts can be recognized as distinct groups of cells in most sections, and hence we regard them as of different parts in this study. Laterally, the Vi is bounded by the Dp (Figs. 6, 7). The cell bodies are medium sized and loosely distributed.

The E is identifiable in the caudal telencephalon above the preoptic area and lies in the ventralmost aspect of the ventral telencephalic area (Figs. 6, 7). Component cells of the E are very small, round, densely packed, and well stained.

Preoptic area.–The preoptic area is the caudalmost region of the telencephalon. Rostrally, it begins as a small periventricular cell mass surrounding the preoptic recess of the third ventricle (V3), a recess ventral to the ac. The preoptic area includes the parvocellular (Pp) and the magnocellular preoptic (Pm) nuclei. The Pp consists of relatively small cells and is subdivided further into the anterior (Ppa) and posterior (Ppp) parts. Lying below the ac, the Ppa faces the preoptic recess (Fig. 4). More caudally, the Ppp appears ventral to the Ppa (Fig. 6, section #140), which also faces the V3. The Ppa cells are loosely distributed and not well stained, while the Ppp cells are slightly smaller than those in the Ppa, densely packed, and well-stained with cresyl violet. The Ppa is replaced ventromedially by the Ppp and dorsally by the Pm (Fig. 7). The Pm is bordered dorsally by the Vp at the rostral level of the nucleus (Fig. 7, section #143) and by the ventromedial thalamic nucleus more caudally (Figs. 7–9). The Pm is bordered ventrally by the Ppp. The Pm cells are spherical and much larger than those in the Pp. The Pm is also a periventricular nucleus facing the V3. The Ppp and Pm are

rostrocaudally elongate, ending caudally at the level of the posterior commissure (pc) (Fig. 9, section #182).

Diencephalon.–The diencephalon is the caudal component of the forebrain, lying between the telencephalon and mesencephalon. The diencephalon of teleosts has been divided into the epithalamus, thalamus, posterior tuberculum, hypothalamus, and synencephalon (Braford and Northcutt 1983). Although recent developmental studies propose that the hypothalamus belongs to the same brain segment (neuromere) as the telencephalon (e.g. Puelles and Rubenstein 2003, 2015), we follow the traditional view in the present study to maintain continuity with the terms in previous literatures. In the diencephalon of actinopterygians, a prominent group of nuclei called the preglomerular complex is present, whose counterpart in other vertebrates remains to be determined. Owing to the ambiguity in identity, therefore, we describe the preglomerular complex under a section, separate from the diencephalic regions mentioned above.

Epithalamus.–Epithalamus contains the pineal organ (epiphysis), parapineal (paraphysis; if present: see Borg et al. 1983; Ishikawa et al. 2015), and habenula (HB). Unfortunately, the pineal and parapineal were lost in the present materials owing to its fragility and will not be demonstrated. The HB appears dorsal to the thalamus, facing the V3. Caudally, the HB stays on the medial margin of the TO, a mesencephalic structure (Fig. 7, section #159; Fig. 8, section #171).

Thalamus.–The thalamus emerges ventral to the HB. It is subdivided further into the dorsal and ventral thalami. The former consists of the anterior (A) and the central (CP) thalamic nuclei, while the latter is composed of the ventromedial (VM) and ventrolateral (VL) thalamic nuclei. The VM is the rostralmost ventral thalamic nucleus that lies ventral to the HB and dorsal to the Pm (Fig. 7, section #159). The VM is laminar rostrally (Figs. 7–9), while a more densely packed cell population joins caudally (Fig. 9, section #193). The former

component of the VM is referred as the rostral VM (VMr), and the latter as the caudal VM (VMc) in the present study. The VMr disappears slightly caudal to the rostral pole of the VMc, and the VMc disappears just caudal to the pc (Fig. 10). Slightly caudal to the rostral pole of the VMr, a more diffuse cell population appears lateral to the VMr. This population of diffuse cell is the VL (Fig. 8). The VL becomes indistinct caudally and disappears at the level of the pc. The rostralmost dorsal thalamic nucleus, or the A appears dorsal to the VMr and ventral to the habenula (Fig. 8, section #171). The A is a laminar nucleus with one or two cell plates and disappears caudally at the level of the pc (Fig. 9, section #182). The cell bodies in the A are small, round, densely packed and well stained with cresyl violet. The CP appears ventral to the periventricular pretectal nucleus (PP) replacing the A (Fig. 9, section #182). Cells in the CP are small to medium in size. Rostrally, the cells in the CP are arranged as a "C"-shaped cell layer (Fig. 9, section #182). Caudally, cells are distributed more laterally and diffusely (Fig. 9, section #193).

Posterior tuberculum.–The posterior tuberculum is derived embryologically from the basal plate regions whose corresponding alar plate derivatives are the dorsal and ventral thalami. The posterior tuberculum lies ventrocaudal to the thalamus in the adult brain, owing to the curvature of the brain axis by the cephalic flexure (Kage et al. 2004). We consider that it is composed of periventricular nucleus of the posterior tuberculum (PPT), posterior tubercular nucleus (NPT), and corpus mamillare (CM) in the present study. According to Braford and Northcutt (1983), the posterior thalamic nucleus (PT), torus lateralis (TLa), and preglomerular complex are also regarded as parts of the posterior tuberculum. However, alar origin of the preglomerular complex has also been proposed (Ishikawa et al. 2007). Due to uncertainty in ontogenetic origin, we describe the latter structures under the subsequent section: "preglomerular complex and other outlying structures". The PPT replaces the VM caudally and is present dorsal to a hypothalamic nucleus (anterior tuberal nucleus: NAT). The

PPT contains densely packed periventricular small cells as well as large cells (Fig. 9, section #201). The CM locates ventral to the commissural preglomerular nucleus (PGc) and dorsal to the diffuse nucleus of the inferior lobe (NDLI: a hypothalamic structure). The CM is round in shape and is further divided into three nuclei: the parvocellular (CMp), dorsal magnocellular (CMmd) and ventral magnocellular (CMmv) nuclei, which can be discriminated on the basis of differences in cell sizes, cell density, and location (Fig. 11). The CMp is a periventricular nucleus and bilateral nuclei are facing closely at the midline. Component cells are small and stained very densely. The CMmv is present ventrolateral to the CMp and contains larger cells that show more diffuse distribution. The cells in the rostralmost zone of CMmv are quite large while the cell size gradually decreases caudally. The CMmd is located dorsolateral to the CMp and ventrolateral to the PGc (Fig. 11). Cells in the CMmd are largest among the three mamillary nuclei. The NPT replaces the NAT caudally. The nucleus is composed of medium-sized cells, and the bilateral nuclei fuse at the midline (Fig. 10).

Preglomerular complex and other outlying structures.–The preglomerular complex is a group of nuclei that spans a considerable rostrocaudal distance in the ventrolateral diencephalon. The complex contains the prethalamic nucleus (PTh), the preglomerular nucleus (PG), and commissural preglomerular nucleus (PGc) in the mackerel. The PTh was identified by Meader (1934) in an acanthopterygian and a subsequent study revealed that the nucleus receives tectal projections and sends fibers to the Dl (Ito et al. 1980). These connections are identical to those of a part of lateral preglomerular nucleus (a component of preglomerular complex) in cyprinids (Northcutt 2006; Yamamoto et al. 2008), and these nuclei are quite likely homologous. Hence, we describe the PTh in this section. Other components of the preglomerular complex (anterior nucleus, lateral nucleus, medial nucleus, and preglomerular tertiary gustatory nucleus) have been identified and described together with connectional data in different teleost species (e.g. Yoshimoto et al. 1998; Yamamoto et al.

2005; Northcutt 2006; Yamamoto et al. 2008; Kato et al. 2011). These studies indicate that preglomerular components with the same connections (hence presumably homologous structures) can be present in different positions within the complex in different species. That is, giving names to preglomerular components in the Japanese jack mackerel, following the terminology of the studies enumerated above, is rather difficult. In the present study, therefore, we identify only clearly distinguishable nuclei. Other components that are difficult to identify with confidence will be tentatively called under a general name "the preglomerular nucleus (PG)".

The rostralmost component of the preglomerular complex is the PTh that appears ventral to the suprachiasmatic nucleus (SCN) and medial to the ventral optic tract (Fig. 8, section #171). The PTh is large and ovoid rostrally, while it becomes more elongate dorsocaudally in more caudal sections (Fig. 9, section #182). Ovoid cell bodies of the nucleus occupy its ventral zone while a neuropil is clearly identifiable dorsally (Fig. 8). As the PTh becomes smaller in caudal sections, the PG appears ventral to the PTh (Fig. 9, section #182) and replaces the PTh ventrally in further caudal sections (Fig. 9, section #193). The PG contains two different components that are composed of larger cells and smaller cells, respectively (Fig. 9, section #193). We do not give different names to these components, as mentioned in the preceding paragraph. The PG shifts medially as the section level goes caudally. The PGc is clearly identifiable as a well-stained, dense cell group (Fig. 10). The cell bodies are smaller than those of PG. The PGc appears medial to the small cell component of the PG. More caudally, it becomes situated medial to the corpus glomerulosum pars rotunda (GR) (Fig. 10, section #210). The PGc may be identified as such on the basis of its position medial to the GR and features of cells common with those of the same-named nucleus in other species. Also, confusing cell groups are not present close to the nucleus. Further caudally, the PGc shifts

medially and finally the PGc on both sides fuse at the midline (Fig. 11), a feature also seen for the PGc of other perciforms (e.g. Nile tilapia: figure 4 of Sawai et al. 2000).

The PT is a small nucleus that appears dorsal to the torus lateralis (TLa) and medial to the GR (Fig. 10, section #210). Medium-sized cell bodies are scattered within the nucleus, which are not densely stained. The TLa locates ventral to the ventromedial margin of the OT (Fig. 9, section #193) and dorsal to the diffuse nucleus of the inferior lobe (NDLI). We can distinguish between the TLa and the NDLI on the basis of the cell density and staining; cells in the TLa are much more aggregated and well stained than those in the NDLI, although component cells appear similar (medium-sized and round). The TLa may be subdivided into two components as has been reported in the Mozambique tilapia (Pepels et al. 2002). Cells in the ventral zone of the TLa are more loosely distributed, and this zone likely corresponds to the inferior subdivision of torus lateralis (TLai) of the latter report (Figs. 9, 10). The TLai is present only at the mid-levels of the torus.

Hypothalamus.–The hypothalamus occupies the ventralmost region of the diencephalon. It is composed of a medial (tuberal) hypothalamic region and a lateral hypothalamic region that is usually referred to as the inferior lobe. The former consists of the SCN, periventricular hypothalamic nucleus (PH), lateral hypothalamus (LH), anterior tuberal nucleus (NAT), nucleus of posterior recess (NRP), and lateral tuberal nucleus (NLT). The latter is composed of the nucleus of lateral recess (NRL), central nucleus of inferior lobe (NCLI), and NDLI.

The rostralmost component of the medial hypothalamic region is the SCN, which is sometimes regarded as a preoptic nucleus. Rostrally, the SCN appears ventrolateral to the Ppa and Ppp, and dorsomedial to the optic tract (Fig. 7, section #143). The nucleus continues caudally up to the level of the HB, occupying a periventricular position (Fig. 8, section #171). This nucleus is composed of relatively small and round cells that are well stained with cresyl violet. The cells are more diffusely distributed in comparison with those in the dorsally

adjacent Ppp. The PH extends along the ventricular surface of the ventral part of V3 (Figs. 9, 10). Cells of the PH are small, round, densely packed and well stained. The LH is present lateral to the PH and ventral to the NAT (Fig. 10, section #201). The cells in the LH are similar to those in the PH, but they are not periventricular. The NAT appears at similar level as the LH (Fig. 10, section #201). It is a triangle-shaped nucleus dorsal to the LH and lateral to the PH. Cells of NAT are larger, more diffuse, and stained paler than those in the PH and LH. The NLT is situated in the ventrolateral zone of the medial hypothalamic region (Figs. 8, 9). The NLT can be divided into the lateral (NLTl) and posterior (NLTp) parts. Rostrally, the NLTl is situated medial to the PTh and is composed of large cells and the bilateral nuclei appear like an inverted "V" (Fig. 8, section#176). Caudally, the bilateral nuclei become well separated (Fig. 9, section #182). The NLTp appears more caudally (Fig. 9, section #193). Most of the cells in this nucleus are small. Although the major component cells of the NLTp are similar to those of PH neurons, the presence of few larger cells differentiate the NLTp from the PH. More caudally, the V3 protrudes laterally to form the posterior recess, and surrounding the recess is the NRP (Fig. 10, section #210). Cells of the NRP are small and well stained.

A large, ventrolateral protrusion of the hypothalamus is the inferior lobe (Figs. 9–11). A sulcus marks the boundary between the inferior lobe and medial hypothalamic region. Rostrally, the inferior lobe is composed only of the NDLI (Fig. 9, section #193). Cells in the NDLI are round, medium-sized, and distributed diffusely as the name of the nucleus implies. A bit caudal to the rostral pole of the inferior lobe, the NRL appears in the center of the lobe. This nucleus is further divided into the lateral NRL (NRLl) and medial (NRLm) subnuclei. The NRLl is a periventricular nucleus surrounding the lateral recess of the third ventricle (Figs. 10, 11). A cell sparse zone or a neuropil surrounds the periventricular cells of NRLl (Fig. 11). Cells in the NRLl are small, densely aggregated, and well-stained. The NRLm

appears dorsomedial to the NRLl and is not periventricular. The NRLm contains loosely distributed medium-sized cells (Fig. 10, section #210). The NCLI appears dorsomedial to the NRLl and is composed of medium-to-large cells that are stained pale with cresyl violet (Figs. 10, 11). A cell sparse zone or a neuropil is present dorsolateral to the NCLI.

Synencephalon.–The synencephalon is the caudalmost segment (or neuromere) of diencephalon and corresponds to the prosomere 1 of Puelles and Rubenstein (2003). It is composed of the pretectum and the synencephalic tegmentum, which are of alar and basal plate origin respectively. Sometimes, the synencephalic tegmentum is considered as a part of the posterior tuberculum.

The pretectum contains the cortical nucleus (C), nucleus pretectalis (NP), intermediate (pretectal) nucleus (Nint), corpus glomerulosum, parvocellular superficial pretectal nucleus (PSp), periventricular pretectal nucleus (PP), nucleus of posterior commissure (PC), nucleus paracommissuralis (NPC), area pretectalis (AP), and subcommissural organ (SCO). The rostralmost pretectal nucleus is the PSp (Fig. 7, section #140), which is embedded in the optic tract (Fig. 6, section #140). The PSp is composed of small cells and neuropil, forming together a sheet like structure that is pleated. The nucleus is rostrocaudally elongate and continues caudally up to the level of HB (Fig. 8, section #171). Close to the caudal margin of the PSp, the C appears medial to the optic tectum (Fig. 7). Neurons of the C are large, ovoid or sometimes fusiform, tightly aggregated, and well-stained. The AP is a cerebellopetal structure (Ito and Yoshimoto 1990) and can be divided into the dorsal (APd) and ventral (APv) parts (Fig. 8, section #171). Component cells of the two parts are similar: round, medium-sized, and loosely distributed. However, a cell sparse zone separates the two parts. The Nint appears ventral to the APv (Fig. 8). The cell bodies in the nucleus are spherical, medium-sized and well stained. The cells are relatively densely packed, accompanying a neuropil. Lateral to the Nint is the NP, (Fig. 8, section #176). The NP is a large nucleus that is

composed of very large and spherical cells. They are stained well with cresyl violet and are quite diffusely distributed within the nucleus. The corpus glomerulosum contains glomeruli as the name implies (see cell-free and round structures within the nucleus; Figs. 10, 11) and is divided into anterior and posterior parts: the GA and GR. The GA appears medial to the NP (Fig. 9, section #182). The GA is composed of large cells and small cells without clear arrangement of component cells. A fiber tract (tractus rotundus: rot; Figs. 9, 10) extends caudally, which is connected caudally with the GR. The GR is composed of large cells and small cells, similarly to the GA. However, the GR is much larger than the GA (Fig. 11). Another element of the pretectum is the SCO, which is clearly identifiable on the ventral surface of the pc (Fig. 9, section #182). The SCO is a periventricular organ and is composed of a sheet of slender cells whose ventral part faces the V3. The PP is a periventricular nucleus surrounding the fasciculus retroflexus (fr), a tract composed of habenulofugal fibers to the interpeduncular nucleus (Figs. 8, 9). Cells of PP are spherical and small. The PC is known as a retinorecipient nucleus, which is located ventrolateral to the pc (Ito et al. 1984) (Fig. 8, section #182). Although we did not investigate retinal projections in the present study, medium-to-large sized spherical cells are present in a scattered manner, which appear to correspond to the neurons of the PC reported in a previous study (Somiya et al. 1992). Therefore, we identify the neuronal populations as such. The NPC is identifiable dorsolateral to the PP (Figs. 8, 9). Cells in the NPC are loosely distributed, medium-sized, and well stained.

The synencephalic tegmentum contains a single conspicuous nucleus or the nucleus of medial longitudinal fasciculus (NFLM). The NFLM appears just caudal to the pc (Figs. 10, 11). The NFLM contains medium-sized, large and very large neurons, most of which are ovoid but some are fusiform.

Discussion

We have prepared a complete forebrain atlas of the Japanese mackerel in the present study. The brain atlas of the brain stem and spinal cord will be presented in a subsequent paper. Together, these brain atlases will cover the entire neuraxis of the mackerel, which will provide the basis on future neurobiological studies in the jack mackerel and other teleosts. Below, we discuss on the forebrain neuroanatomy of the Japanese jack mackerel, comparing with other teleosts and paying attention to the features unique to the mackerel. Those structures that do not require special mention will not be discussed below.

Prior to discussion on the cytoarchitecture of the forebrain, we will briefly consider about the external brain morphology of the Japanese jack mackerel. The brains of teleosts sometimes show hypertrophied brain regions, which is usually related to well-developed sensory systems. For example, the olfactory bulb of the moray eel *Gymnothorax kidako* is extremely large (Ito et al. 2007), reflecting the huge olfactory epithelium of this species. Similarly, the vagal lobe (primary gustatory center) of the common carp *Cyprinus carpio* is a huge bulge due to the presence of numerous taste buds in the pharynx (Ito et al. 2007). Although the brain of the Japanese jack mackerel did not exhibit such amazing enlargements as enumerated above, the TO, CrC, and CC show moderate hypertrophies. The TO is the largest primary visual center in teleosts, and vision may be rather important for the survival of the Japanese jack mackerel. This interpretation is supported by previous reports on the specialized feature of the retina in the genus *Trachurus*. Visual cells in the retina of the Pacific jack mackerel *Trachurus symmetricus* show a specialized arrangement that serves for higher visual abilities for moving objects (Arimoto et al. 2010). The inner plexiform layer of the retina in the Mediterranean horse mackerel *Trachurus mediterraneus* is highly

differentiated and contains not less than 25 sublayers (Podugolnikova 1985), suggesting well-developed visual capabilities of *Trachurus*. The CrC is a layer of neuropil that covers the nucleus medialis of rhombencephalic octavolatral area, which is the largest among the primary lateral line centers (Yamamoto et al. 2010). The CC is involved in the motor control (Tuge 1934). Moderate hypertrophies of the latter structures may reflect importance of lateral line information and requirement of precise motor control for shoaling behavior.

Telencephalon.

Olfactory bulb.–The OB of the Japanese jack mackerel is of the sessile-type. The sessile OB is the major type in teleosts, which can be found in anguilliforms like the Japanese eel (Mukuda and Ando 2003), cypriniforms such as the zebrafish (Wullimann et al. 1996), salmoniforms such as the rainbow trout (Meek and Nieuwenhuys 1998), beloniforms such as the medaka (Ishikawa et al. 1999; Kage et al. 2004), and in other percomorphs such as a cichlid (Fernald and Shelton 1985) and butterflyfishes (Bauchot et al. 1989; Dewan and Tricas 2014). The olfactory bulb of the stalked type is minor (e.g. cyprinids, silurids, gadids: Tuge et al. 1968) and shows a sporadic pattern of phylogenetic distribution. For example, the bulb of the goldfish is of a stalked type (Rupp et al. 1996), unlike the zebrafish, although both species are cyprinids.

Four layers are recognized in the Japanese jack mackerel as in other teleosts: e.g. the zebrafish (Wullimann et al. 1996) and the goldfish (Ichikawa 1976). This laminar organization as well as component cells of each layer is in agreement with almost all other species of teleosts, except anguilliforms where glomeruli and granule cell aggregates show scattered distribution throughout the bulb (Ito and Yoshimoto 1991). A recent brain atlas of the pebbled butterflyfish by Dewan and Tricas (2014) divided the olfactory bulb into five concentric laminae, where the secondary olfactory layer (a layer of bulbar efferent fibers and telencephalo-bulbar fibers) was additionally recognized. This layer was not clearly recognized

in the present study of the Japanese jack mackerel. This is presumably because it is not well developed in this species although these fibers are present in this species.

Dorsal telencephalic area.–The present study divided the dorsal telencephalic area into five parts (Dl, Dm, Dc, Dd, and Dp) and the nT, which are also recognized in other perciforms, such as the European sea bass (Cerdá-Reverter et al. 2001a), a cichlid *Astatotialapia burtoni* (Burmeister et al. 2009), the dwarf snakehead (Baile and Patle 2011), and the pebbled butterflyfish (Dewan and Tricas 2014). Such divisions were also demonstrated in other actinopterygian fishes (Peter and Gill 1975; Nieuwenhuys 1982; Wullimann et al. 1996; Ishikawa et al. 1999; Butler 2000; Northcutt 2006), although the Dp was not mentioned in the goldfish (Peter and Gill 1975), the Japanese eel (Mukuda and Ando 2003) and *Notobranchius* (D'Angelo 2013). A region corresponding to the Dp may be included in the Dl in the latter studies. Among the dorsal telencephalic parts of the Japanese jack mackerel, the Dl is the most complex and could be subdivided into 7 regions. Traditionally, the Dl has been divided into a few regions (*Scleropages formosus*: Nieuwenhuys 1962; *Sebastiscus marmoratus*: Murakami et al. 1983). In more recent studies in percomorph teleosts, however, the Dl is sometimes subdivided into four (Cerdá-Reverter et al. 2001a) or five regions (Dewan and Tricas 2014; Burmeister et al. 2009). In contrast, just a few regions are recognized in cyprinids and the medaka even in recent studies (Northcutt 2006; Yamamoto and Ito 2008; Ishikawa et al. 1999). Therefore, the number of recognizable regions of the Dl appears to show species differences. It should be also mentioned that some Dl regions may not be recognizable with conventional methods such as Nissl staining, due to underdevelopment of each region. Owing to the presence of large species differences, one-to-one comparisons of different Dl regions among different fish species are quite difficult at present. Neurochemical analyses with immunohistochemistry, as has been done by Dewan and Tricas (2014), may lead to the finding of such "hidden" regions. Non-the-less, the

presence of as many as seven clearly recognizable subregions suggests that the Dl of the Japanese jack mackerel is very well differentiated. The Dl is known to receive visual information in other teleosts (Ito et al. 1980; Northcutt 2006; Yamamoto and Ito 2008). This feature, together with the hypertrophied TO, suggests the importance of visual information for the Japanese jack mackerel. The most interesting Dl region in the Japanese jack mackerel is the Dl2, which appears rostrally as an island separate from the rest of the Dl and becomes fused with the dorsal telencephalic area, caudally. This indicates that the Dl2 is protruded rostrally as a bulge. The precise functional significance of this feature, however, remains unclear.

The Dm was subdivided into dorsal (dDm) and ventral (vDm) regions in the present study. The terminology of the Dm suffers from inconsistencies in different studies, and some notes are provided below to avoid further confusion in future studies. Some studies subdivided the Dm into dorsal and ventral components (Murakami et al. 1983; Ishikawa et al. 1999; Pepels et al. 2002; Yamamoto and Ito 2005, 2008), as we have done in the present study of the Japanese jack mackerel. Such a dorsoventral subdivision is not made in other studies (Peter and Gill 1975; Bass 1981; Maler et al. 1991; Corrêa et al. 1998; Cerdá-Reverter et al. 2001; Mukuda and Ando 2003; Baile and Patle 2011; D'Angelo 2013; Dewan and Tricas 2014), although the region corresponding to our vDm appears to be included within the Dm. Still other studies regarded our vDm as a region within the ventral telencephalic area: Vd (Northcutt 2006) or Vs (Burmeister et al. 2009). Although we followed our way of terminology in the present report, renaming might perhaps become necessary by future studies that unravel dorsal or ventral telencephalic identity of the vDm. The dDm was further subdivided into two subregions, dDm1 and dDm2, in the present study. Northcutt (2006) subdivided the Dm (= our dDm) into rostral and caudal components in the goldfish. The dDm1 and dDm2 occupy rostral and caudal zones of the Dm, and the two Dm regions in the

Japanese jack mackerel and goldfish might be homologous. The dorsal telencephalic region that corresponds to our dDm is not subdivided in some studies (e.g. Peter and Gill 1975; Bass 1981; Maler et al. 1991; Ishikawa et al. 1999; Mukuda and Ando 2003), while other studies do recognize three subregions (Burmeister et al. 2009; Dewan and Tricas 2014). Thus, as in the case for the Dl, further studies are necessary to compare precisely the dDm subregions among different teleost species. The dDm is known to receive sensory inputs from the proglomerular complex in the diencephalon (Yamamoto and Ito 2005, 2008; Northcutt 2006). Species differences in the complexity of dDm organization might perhaps be related to the species differences in the development of sensory systems. The vDm could be subdivided into three regions in the Japanese jack mackerel while such subdivisions were not recognized in previous studies (see above). The reason for the species differences remains an open question. Also interestingly, the left and right vDms fuse at the midline in the Japanese jack mackerel. Such a fusion was also found in the snakehead (Baile and Patle 2011) and dwarf gourami (figure 11 of Yamamoto et al. 2000). Such midline fusions may facilitate information exchanges between the bilateral Dm, although precise significance remains to be elucidated.

The Dc is present in the central zone of the dorsal telencephalic area. Similarly to the situations of the Dm and Dl, the Dc has also been divided into different numbers of subdivisions in a number of species: e.g. four subregions in *Nothobranchius* (D'Angelo 2013) and two subregions in a snakehead (Baile and Patle 2011). Three subdivisions were recognized in the present study in the Japanese jack mackerel, and one-to-one comparison of Dc subregions is not an easy task to accomplish.

The Dd has been identified in between the Dm and Dl, which is composed of small cells (Nieuwenhuys 1962). The identification of the Dd may differ among different studies. For example, the Dd of Yamamoto and Ito (2005) and Northcutt (2006) identified in the goldfish is composed of medium-sized cells. Recently, the Dd of *Gymnotus* and *Apteronotus* was

analyzed in detail, and two subdivisions of small cells and one subdivision of larger cells were recognized (Giassi et al. 2012). In the present study, we have identified a subdivision of small cells (Dd) and another subdivision of larger cells (Ddmg). The Ddmg may correspond to D.c.d. of Nieuwenhuys (1962), which is composed of scattered large cells and is regarded as a subregion of Dc.

Ventral telencephalon and preoptic area.–Most of the ventral telencephalic parts seen in other teleosts were recognized in the Japanese jack mackerel: Vv, Vd, Vl, Vs, Vp, and Vi. In many teleosts, an aggregate of small cells is present lateral to the Vd and Vv and is called the central part of the ventral telencephalic area (Vc) (Maler et al. 1991; Corrêa et al. 1998; Northcutt 2006; Burmeister et al. 2009; Baile and Patle 2011; D'Angelo 2013; Dewan and Tricas 2014). Such a population of cells was not found in the Japanese jack mackerel in the present study, similarly to the situation in the Japanese eel (Mukuda and Ando 2003). The Vc is considered as laterally migrated cells that are related to the cells in the Vd and/or Vv (Northcutt and Davis 1983), and the lack of recognizable Vc may reflect less pronounced migration or less condensed distribution of cells in the Japanese jack mackerel and the Japanese eel. Only in some actinopterygians (*Polypterus*, *Ictarulus*, *Gymnotus*, and *Lepomis*), a relatively cell-poor ventral telencephalic zone was identified and was called the Vn (= V'nother') (Bass 1981; Northcutt and Davis 1983). Such a zone was not recognized in the Japanese jack mackerel, similarly to the situation in most teleosts reported in previous studies. Finally, a recent study in the pebbled butterflyfish (Dewan and Tricas (2014) reported a new part of the ventral telencephalic area that was termed the cuneate nuleus (Vu). The Vu of Dewan and Tricas (2014) was present between their Dm4 and Dp. Such a structure has not been recognized in the Japanese jack mackerel studied here or in those reports on other actinopterygians. The presence of Vu in the pebbled butterflyfish is of particular note, which might perhaps be related to some sort of specialized functions unique to butterfly fishes. The

nuclei in the preoptic area have been termed in a variety of ways in those reports cited above. However, dividing the area into small celled (parvocellular) and large celled (magnocellular) components and subdividing parvocellular population into anterior and posterior groups, as we have done in the present study, are relatively well accepted. Various neurochemical substances including peptides and catecholamine are present in the preoptic area (Yamamoto et al. 1998; Filippi et al. 2010). Comparisons between species at finer levels would require neurochemical data in different species of teleosts.

Diencephalon.

Epithalamus and Thalamus.–Traditionally, the dorsal thalamus has been subdivided into the dorsomedial and dorsolateral thalami while the ventral thalamus into the ventromedial and ventrolateral thalami (Schnitzlein 1962). This terminology was followed by Peter and Gill (1975) and Peter et al. (1975), although a ventrolateral thalamic nucleus was not identified in these studies in the goldfish and a killifish. Later on, Braford and Northcutt (1983) proposed a new scheme of thalamic terminology, in which the dorsal thalamus was subdivided into the anterior (A), central posterior (CP), and dorsal posterior (DP) thalamic nuclei, while the ventral thalamus into ventromedial (VM), ventrolateral (VL), and intermediate thalamic nuclei. The latter terminology has been adopted in most of subsequent studies including the present study (Fernald and Shelton 1985; Striedter 1990; Maler et al. 1991; Butler and Northcutt 1993; Wullimann et al. 1996; Cerdá-Reverter et al. 2001b; Mukuda and Ando 2003; D'Angelo 2013). However, subtle differences can be found. The intermediate thalamic nucleus, which is present in between the anterior thalamic nucleus and ventromedial thalamic nucleus (Braford and Northcutt 1983), was not found in some species (Japanese eel: Mukuda and Ando 2003; *Apteronotus*: Maler et al. 1991; the present study). Rostrally, the cells of VM form rows of cells or cell plates while cells form an aggregate in the caudal zone of the nucleus in the Japanese jack mackerel. Therefore, the VM was divided into rostral (VMr) and

caudal (VMc) components in the present study, as has been done in the channel catfish (Striedter 1990) and goldfish (Yamamoto and Ito 2008). We have included a cell population, which appears to correspond to the DP of Braford and Northcutt (1983) (see their figure 16), into a dorsally located nucleus, the periventricular pretectal nucleus (PP). This was done based on the following reasons: 1) The cell population in question appears very similar to those of the periventricular pretectal nucleus; 2) Cells dorsal to the fasciculus retroflexus (periventricular pretectal nucleus of Braford and Northcutt (1983)) are dopaminergic (zebrafish: Yamamoto et al. 2011), while cells ventral to the fasciculus (DP of Northcutt and Braford (1983)) are serotoninergic (zebrafish: Kaslin and Panula 2001), and 3) The two monoaminergic cell populations are continuous surrounding the fasciculus retroflexus (Yamamoto et al. 2011). Neurochemical studies and detailed observation of this brain region in other species are important to support or refute our tentative interpretation.

Posterior tuberculum.–The organization of the posterior tuberculum of the Japanese jack mackerel is in basic agreement with previous reports that analyzed this region in detail (goldfish: Braford and Northcutt 1983; zebrafish: Wullimann et al. 1996). However, possible species differences were noted as to the corpus mamillare (CM). The CM of the two cyprinid species (and other studies mentioned in the preceding section) was not divided further into nuclei. However, the CM of the Nile tilapia could be divided into two large-celled nuclei (with different fiber connections) and one small-celled nucleus (Sawai et al. 2000). Our careful observations resulted in finding similar three nuclei in the Japanese jack mackerel. Similar subnuclei were not identified in previous studies in other perciforms (e.g. *Astatotilapia*: Fernald and Shelton 1985), and the presence of multiple subnuclei of the CM may not be a shared character in perciforms. Alternatively, further detailed observations may result in finding nuclei that were unrecognized in previous studies. Somewhat surprisingly, the CM was not described in *Apteronotus leptorhynchus* (see Maler et al. 1991) and

Nothobranchius furzeli (see D'Angelo 2013). These negative findings may be due to underdevelopment of the CM in these species and resultant oversights.

Preglomerular complex and other outlying structures.–The preglomerular complex, which is located ventrolateral to the thalamus, has been divided into several nuclei or parts: the anterior (PGa), lateral (PGl), medial (PGm), and commissural (PGc) preglomerular nuclei in the goldfish (Braford and Northcutt 1983). Subsequent studies indicated that the preglomerular complex is the major diencephalic relay station of various sensory modalities to the dorsal telencephalon (for details see Yamamoto and Ito 2005, 2008; Northcutt 2006, and literatures cited in these papers). Braford and Northcutt (1983) proposed that the nucleus glomerulosus of Peter and Gill (1975) in the goldfish [also called the nucleus rotundus (Sheldon 1912) in the carp] is a component of the preglomerular complex on the basis of its reception of tertiary gustatory projections from the secondary gustatory nucleus (Morita et al. 1980). The tertiary gustatory nucleus in the preglomerualr complex is currently called the preglomerular tertiary gustatory nucleus (pTGN) to make clear its preglomerular identity (goldfish: Kato et al. 2012; Nile tilapia: Yoshimoto et al. 1998). More recently, a nucleus was found within the preglomerular complex that receives general visceral sensory information (sensory information from the gut) and is called the preglomerular general visceral nucleus (pVN) (goldfish: Uezono et al. 2015; Nile tilapia: Yoshimoto and Yamamoto 2010).

The nucleus prethalamicus of Meader (1934; PTh), which has long been known as a visual relay nucleus to the dorsal telencephalon (Ito et al. 1980; Ito and Vanegas 1983, 1984) and is found in acanthopterygians (Shimizu et al. 1999; Imura et al. 2003), is now considered a component of the preglomerular complex (Northcutt 2006; Yamamoto and Ito 2008). The PTh is present rostral to the thalamus, as the name implies, and is the rostralmost structure among the preglomerular components in acanthopterygians. Thus, preglomerular components were named after their topographical positional relationships, except the pTGN and pVN that

were named on the basis of the sensory modality that they receive. Unfortunately, naming based on positions and erroneous assumptions in homology led to confusions. Firstly, the PTh of acanthopterygians is frequently called PGa (e.g. Fernald and Shelton 1985; D'Angelo 2013), a name defined first for the goldfish nucleus (Braford and Northcutt 1983). This was done because the PTh of acanthopterygians and PGa of cyprinids were assumed to be homologous; both occupy the most rostral zone among the preglomerular components. Due to this assumption, the PGa of the goldfish was once considered to relay visual information like the PTh of acanthopterygians (Wullimann and Mueller 2004). However, it turned out later that the PGa of cyprinids relays auditory information to the dorsal telencephalon (Yamamoto and Ito 2005; Northcutt 2006). In the goldfish a visual relay region was found within the PGl, not PGa (Northcutt 2006; Yamamoto and Ito 2008). Thus, the term PTh should be kept for acanthopterygians, and the name "PGa" should not be used for this acantopterygian nucleus. It should be also mentioned that the preglomerular complex can be poorly differentiated in some teleosts, and subdivisions were not defined in the Japanese eel (Mukuda and Ando 2003). Similarly, Butler and Northcutt (1993) only defined the PGm and PGl that may contain other preglomerular structures within them. The problems mentioned above indicated that connectional data are quite helpful to analyze homology of preglomerular structures. In the present study of the Japanese jack mackerel, an acanthopterygian, we could clearly identify the PTh that is present ventromedial to the optic tract and accompanies well-developed neuropil: characters seen in other acanthopterygians. The PGc could also be identified, whose caudalmost regions on both sides fuse at the midline. Other components of the preglomerular complex, however, could not be distinguished. Although the presence of large-celled and small-celled portions was recognized, we called the rest of the preglomerular complex simply the PG. Presumably, the PG of the Japanese jack mackerel contains nuclei that relay auditory, lateral line, gustatory, and general visceral senses to the dorsal telencephalon.

The torus lateralis (TLa: also called the nucleus of TLa) has long been regarded as of single entity. However, Pepels et al. (2002) distinguished the ventral zone of TLa as the inferior subdivision of TLa (TLai) in the Mozambique tilapia, on the basis of cytoarchitecture. A similar subdivision was also identified in the Nile tilapia on the basis of connectional differences and cytoarchitecture (Yang et al. 2007; Yoshimoto and Yamamoto 2010). The TLai was identified in the present study of the Japanese jack mackerel, indicating that this subdivision is not a specialized character in tilapias but may be shared with other perciform fishes.

Hypothalamus.–The hypothalamus is composed of medial (tuberal) and lateral (inferior lobe) regions. There are two major styles of terminology for hypothalamic structures. One calls most of the tuberal region the nucleus lateralis tuberis (NLT) and subdivides it into several parts such as anterior, posterior, lateral, and inferior (Peter and Gill 1975). Other structures present in the tuberal regions are the nucleus of posterior recess (NPR) and nucleus of vascular sac. The inferior lobe is divided into diffuse nucleus (NDLI) and nucleus of lateral recess (NRL). The other style of terminology distinguishes periventricular and migrated (present away from the ventricle) hypothalamic structures (Braford and Northcutt 1983). The periventricular hypothalamus is divided into dorsal, ventral, and caudal zones. The dorsal zone corresponds to the NRL (of Peter and Gill 1975), the ventral zone to the NLT (anterior and posterior parts), and the caudal zone to the NLT (inferior part), NPR, and nucleus of vascular sac. Braford and Northcutt (1983) recognized additional hypothalamic structures: ventral tuberal nucleus, lateral hypothalamus (LH), and central nucleus of inferior lobe (NCLI). The ventral tuberal nucleus of Braford and Northcutt (1983) probably corresponds to the lateral part of NLT of Peter and Gill (1975).

Among subsequent studies, Mukuda and Ando (2003) followed the terminology of Peter and Gill (1975). The terminology of Braford and Northcutt (1983) was adopted in most of

other studies (Fernald and Shelton 1985; Striedter 1990; Wullimann et al. 1996; Cerdá-Reverter et al. 2001b). Maler et al. (1991) adopted mixed styles of terminology by distinguishing medially situated periventricular hypothalamic nuclei from the nucleus of lateral recess. We followed the style of Peter and Gill (1975) with minor modifications; we recognized the LH and NCLI of Braford and Northcutt (1983). The reason why we mainly followed the terminology of Peter and Gill (1975) is that periventricular hypothalamic nuclei of Braford and Northcutt (1983) extends considerable mediolateral and/or rostrocaudal dimensions, and it is sometimes difficult to specify the location of a structure in question with the latter terminology.

Synencephalon.–The forebrain atlas of Peter and Gill (1975) did not cover the entire synencephalon, and most of brain atlases followed the terminology of synencephalon defined by Braford and Northcutt (1983). We have adopted several terms of Braford and Northcutt (1983), while some classic terms were also kept. Braford and Northcutt (1983) divided the pretectum into periventricular (close to the ventricle), central, and superficial (close to the meningeal surface) zones. Establishing the notion of the three zones made clearer interpretation of the pretectum, and we accepted this framework. According to Braford and Northcutt (1983), the periventricular pretectal nucleus is composed of dorsal and ventral parts. However, the dorsal part is apart from the third ventricle, and this region probably corresponds to the nucleus of posterior commissure (PC) that receives retinal projections (Ito et al. 1984) and sends fibers to the Edinger-Westphal nucleus (Somiya et al. 1992). The ventral part of periventricular nucleus does not receive retinal projections (Braford and Northcutt 1983), indicating heterogeneity with the dorsal part. Therefore, we kept the term the nucleus of posterior commissure in the present study. Our area pretectalis pars dorsalis might likely correspond to the central pretectal nucleus of Braford and Northcutt (1983), and our area pretectalis pars ventralis might perhaps correspond to the nucleus of basal optic root of

Braford and Northcutt (1983). To be clear about the latter comparison, we have to investigate optic nerve projections in the Japanese jack mackerel, since the nucleus of basal optic root receives retinal projections. Braford and Northcutt (1983) identified two structures in the superficial pretectum of the goldfish: magnocellular superficial pretectal nucleus (PSm) and parvocellular superficial pretectal nucleus (PSp). A structure corresponding to the PSp of the goldfish was identified in the present study of the Japanese jack mackerel. The PSm of cyprinids is a large nucleus embedded in the optic tract, mainly composed of large cells, and projects to the lateral valvular nucleus and CM (Northcutt and Braford 1984; Ito and Yoshimoto 1990; Yoshimoto and Ito 1993). In acanthopterygians, a large nucleus composed of large cells, which has traditionally been called the nucleus pretectalis (NP; Schnitzlein 1962), is present in a position similar to that of PSm of cyprinids. These nuclei were assumed to be homologous and the NP of acanthopterygians was renamed the PSm (Striedter and Northcutt 1989). However, the acanthopterygian nucleus in question projects to the nucleus isthmi, which is present in the rhombencephalic isthmus (Striedter and Northcutt 1989). It should also be mentioned that there are glomerular structures (round structures composed of dendrites and axons terminating on the dendrites) in the PSm of cyprinids, while such structures were not seen in the NP of acanthopterygians (Yoshimoto and Ito 1993). In short, the PSm of cyprinids and NP of acanthopterygians do not appear to be homologous. A subsequent study in the Nile tilapia, an acanthopterygian, reported that the corpus glomerulusum pars anterior (GA) of Brickner (1929) projects to both the lateral valvular nucleus and CM (Yang et al. 2004). Furthermore, the GA possesses glomerular structures and is likely homologous to the PSm of cyprinids. It is premature to conclude that the PSm of cyprinids and the GA of acanthopterygians are in fact homologous, and we keep to the term GA in acanthopterygian fishes.

Some of the pretectal nuclei receive retinal projections, and there are populations of cells that project to the retina (Deguchi et al. 2005). Also, different pretectal nuclei exhibit different connectivity with optic tectum (Kinoshita et al. 2006). Furthermore, only some pretectal nuclei project to the cerebellum while others do not (Uchiyama et al. 1988). Thus, the pretectum contains a number of nuclei with different connectivity and hence function and can potentially be subdivided into larger number of subdivisions than currently recognized. Studies on connections in a single species including the Japanese jack mackerel would promote understanding this brain part.

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Figure legends

Fig. 1 Lateral view of the Japanese jack mackerel (a), and dorsal view of the brain (b) and corresponding line drawing (c). The scale bar in (c) applies for (b)

Fig. 2 Ventral view of the Japanese jack mackerel brain (a) and corresponding line drawing (b), and lateral view (c) and corresponding line drawing (d). Section numbers in Figs. 2–10 are indicated in (d). Scale bars in (b) and (d) apply for (a) and (c), respectively

Fig. 3 Transverse sections through the olfactory bulb and rostral telencephalon of the Japanese jack mackerel. Photomicrographic images are shown on the right, and nuclear boundaries are indicated on the left

Fig. 4 Transverse sections through the rostral telencephalon of the Japanese jack mackerel. Conventions are the same as in Fig. 3

Fig. 5 Transverse sections through the commissural and postcommissural telencephalon of the Japanese jack mackerel. Conventions are the same as in Fig. 3

Fig. 6 Transverse sections through the caudal telencephalon of the Japanese jack mackerel. Conventions are the same as in Fig. 3

Fig. 7 Transverse sections through the caudal telencephalon and rostral diencephalon of the Japanese jack mackerel. Conventions are the same as in Fig. 3

Fig. 8 Transverse sections through the thalamus of the Japanese jack mackerel. Conventions are the same as in Fig. 3

Fig. 9 Transverse sections through the caudal thalamus of the Japanese jack mackerel. Conventions are the same as in Fig. 3

Fig. 10 Transverse sections through the caudal thalamus and rostral synencephalon of the Japanese jack mackerel. Conventions are the same as in Fig. 3

Fig. 11 Transverse sections through the synencephalon of the Japanese jack mackerel.

Conventions are the same as in Fig. 3

Table 1 List of abbreviations

A	anterior thalamic nucleus	PC	nucleus of posterior commissure
ac	anterior commissure	pc	posteroir commissure
APd	dorsal part of area pretectalis	PG	preglomerular nucleus
APv	ventral part of area pretectalis	PGc	commissurall preglomerular nucleus
C	cortical nucleus	PH	periventricular hypothalamic nucleus
CC	corpus cerebelli	Pm	magnocellular preoptic nucleus
CM	corpus mamillare	poc	postoptic commissure
CMmd	dorsal magnocellular nucleus of CM	PP	periventricular pretectal nucleus
CMmv	ventral magnocellular nucleus of CM	Pp	parvocellular preoptic nucleus
CMp	parvocellular nucleus of CM	Ppa	anterior part of Pp
CP	central posterior thalamic nucleus	Ppp	posterior part of Pp
CrC	cerebellar crest	PPT	periventricular posterior tubercular nucleus
dDm	dorsal region of Dm	PR	preoptic recess of third ventricle
dDm1-2	subregions 1-2 of dDm	PSp	parvocellular superficial pretectal nucleus
Dc	central part of dorsal telecephalic area	PT	posterior thalamic nucleus
Dd	dorsal part of dorsal telencephalic area	PTh	prethalamic nucleus
Ddmg	magnocellular region of Dd	rDcl	rostrolateral zone of Dc
Dl1-7	regions 1-7 of Dl	rDcm	rostromedial zone of Dc
Dm	medial part of dorsal telencephalic area	rot	tractus rotundus
dot	dorsal optic tract	SC	spinal cord
Dp	posterior part of dorsal telencephalic area	SCN	suprachiasmatic nucleus
E	entopeduncular nucleus	SCO	subcommissural organ
fr	fasciculus retroflexus	SPV	stratum periventriculare (of optic tectum)
GA	corpus glomerulosum pars anterior	SV	vascular sac
GCL	granule cell layer (of olfactory bulb)	td	torodiencephalic tract
GL	granular layer (of cerebellum)	TE	telencephalon
GLvl	granular layer of VCl	TL	torus longitudinalis
GLvm	granular layer of VCm	TLa	torus lateralis
GR	corpus glomerulosum pars rotunda	TLai	inferior subdivision of torus lateralis
GRL	glomerular layer (of olfactory bulb)	TNggl	ganglion of terminal nerve
HB	habenula	TO	optic tectum
LI	inferior lobe	TOd	dorsal lobe of TO
LH	lateral hypothalamus	TOv	ventral lobe of TO

ll	lateral lemniscus	tpc	tractus pretectocerebellaris anterior
ML	mitral cell layer (of olfactory bulb)	TS	torus semicircularis
MTN	mesencephalic trigeminal nucleus	TSc	central nucleus of TS
MPN	medial pretoral nucleus	TSe	external nucleus of TS
NAT	anterior tuberal nucleus	TSvl	ventrolateral nucleus of TS
NCLI	central nucleus of inferior lobe	TV	telencephalic ventricle
NDLI	nucleus diffuse of inferior lobe	VC	cerebellar valvula
NFLM	nucleus of medial longitudinal fasciculus	VCl	lateral lobe of VC
Nint	intermediate (pretectal) nucleus	VCm	medial lobe of VC
NLT	lateral tuberal nucleus	Vd	dorsal part of ventral telencephalic area
NLTl	lateral part of NLT	vDm	ventral region of Dm
NLTp	posterior part of NLT	vDm1-3	subregions 1-3 of vDm
NP	nucleus pretectalis	Vi	intermediate part of ventral telencephalic area
NPC	nucleus paracommissuralis	Vl	lateral part of ventral telencephalic area
NPT	posterior tuberal nucleus	VL	ventrolateral thalamic nucleus
NRG	nuclues ruber of Goldstein (1905)	VM	ventromedial thalamic nucleus
NRL	nucleus of lateral recess	VMc	caudal part of VM
NRLl	lateral subnucleus of NRL	VMr	rostral part of VM
NRLm	mediall subnucleus of NRL	vot	ventral optic tract
NRP	nuclues of posterior recess	Vp	postcommissural part of central telencephalic area
nT	nucleus taenia	VPN	ventral pretoral nucleus
OB	olfactory bulb	Vs	supracommissural part of ventral telencephalic area
olt	olfactory tract	Vv	ventral part of of ventral telencephalic area
ot	optic tract	II	optic nerve
P	pituitary		