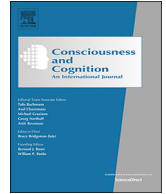




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Review article

Amphioxus neurocircuits, enhanced arousal, and the origin of vertebrate consciousness

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ABSTRACT

Gene expression studies have recently identified the amphioxus homolog of a domain comprising the combined caudal diencephalon plus midbrain, regions implicated in locomotory control and some forms of primary consciousness in vertebrates. The results of EM-level reconstructions of the larval brain of amphioxus, reviewed here, highlight the importance of inputs to this region for light and physical contact, both of which impinge on the same synaptic zone. The neural circuitry provides a starting point for understanding the organization and evolution of locomotory control and arousal in vertebrates, and implies that one of the tasks of midbrain-based consciousness, as it first emerged in vertebrates, would have been to distinguish between light and physical contact, probably sharp pain in the latter case, by assigning different qualia to each. If so, investigating midbrain circuitry more fully could lead to a better understanding of the neural basis of some forms of sensory experience.

1. Introduction

The cephalochordate amphioxus (*Branchiostoma*) is now considered the closest living proxy for the ancestral chordate condition, and is hence an organism of considerable comparative and evolutionary interest (Gee, 2018; Holland, 2015). It is especially relevant to studies on the organization and circuitry of the central nervous system (CNS), as the expression patterns of developmentally important genes are substantially conserved between the amphioxus CNS and that of vertebrates (Holland, 2009; Holland et al., 2013). This makes amphioxus especially valuable as a model for early CNS development, and means the development of early brain circuits can, in principle, be studied in a context that is far less complex than in any vertebrate.

In comparing the regional subdivision of amphioxus and vertebrate brains, a persistent problem has been to identify amphioxus homologs of the telencephalon and midbrain. Amphioxus lacks the expanded dorsal structures (e.g. cortices) that make these regions anatomically distinctive in vertebrates, as well as the sense organs whose input such structures evolved to serve. In young amphioxus larvae there are in fact no neurons in the dorsal nerve cord forward of the lamellar body, a pineal homolog, which is where any counterpart of telencephalon would be located. In older larvae, however, this same region receives dorsally directed branches from the rostral nerves (Lacalli, 2002a, 2004), a possible indication of a late-developing olfactory pathway. The olfactory system and telencephalon are generally considered vertebrate innovations (Satoh, 2005), but amphioxus has a complement of olfactory-related genes (Churcher & Taylor, 2010). A rudimentary homolog of the olfactory bulb may thus be present in older amphioxus larvae and

Abbreviations: ADBs, anterior group of dorsal bipolar neurons; C, enteropneust collar; CNS, central nervous system; Di, caudal diencephalon (thalamus and pretectum); DN, anterodorsal nerve; ESCs, epithelial sensory cells; inf, infundibular cells; IsO, isthmic organizer; JCs, Joseph cells; LPNs, large paired neurons (pairs 1 and 3); LMB, lamellar body; Mes, midbrain; MLR, mesencephalic locomotor region; PMC, primary motor center; psz, primary synaptic zone; RN, rostral nerve; TEM, transmission electron microscopy; Zli, zona limitans intrathalamica

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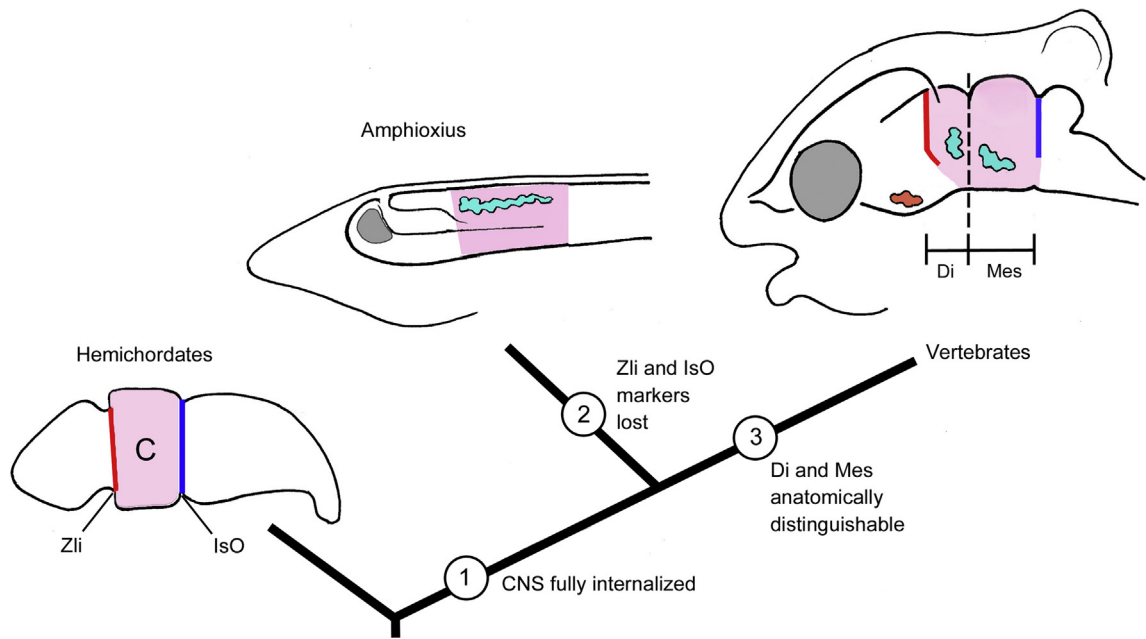


Fig. 1. Evolutionary continuity of the dien-mesencephalon. A comparison of comparable neural domains in developing stages of a hemichordate, amphioxius and an amniote vertebrate, showing the dien-mesencephalon (in pink), which, for vertebrates, corresponds with the domain lying between the *zona limitans interthalamica* (Zli, vertical red line) and isthmic organizer (IsO, vertical blue line) and, in hemichordates, their homologs. The nervous system in hemichordates is largely intraepithelial, so the comparable domain there is the collar epithelium (C). In amphioxius, this zone is also the location of populations of dopaminergic neurons (green) corresponding to those found in the caudal diencephalon (Di) and midbrain (Mes) of vertebrates, and also (not shown) in the collar of hemichordates. There is currently no evidence in amphioxius for homologs of vertebrate hypothalamic dopaminergic nuclei (orange). It is also not known whether the absence of a fully internalized CNS in hemichordates is a secondary simplification, or reflects the ancestral condition, with internalization occurring early in the chordate lineage as shown here. Other abbreviations: 1–4, character states; CNS, central nervous system. Modified from Zieger et al. (2017). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

adults, but if so, it develops too late to play a role in early-stage larval behavior.

In contrast to the telencephalon, a good deal more is known about the amphioxius homolog of the midbrain. From the expression patterns of genes required for CNS regionalization, this is now considered part of a larger domain, the dien-mesencephalic primordium (Albuixechi-Crespo et al., 2017), roughly equivalent to the posterior cerebral vesicle as defined anatomically. This domain includes the amphioxius homologs of the thalamus, pretectum and midbrain, and extends from the cluster of infundibular cells marking the junction between the anterior and posterior cerebral vesicle to approximately the end of somite 1. The corresponding region in vertebrate brain is the zone between the *zona limitans intrathalamica* and the isthmic organizer (Fig. 1), and though markers for these two signaling centers are absent in amphioxius, they are present in hemichordates (Pani et al., 2012), indicating the dien-mesencephalon homolog there is the collar epithelium, which is neurogenic. The implication is that the dien-mesencephalon represents an identifiable subdomain within the nervous system of deuterostomes that predates the origin of chordates, and is retained in amphioxius despite the absence of markers for the signaling centers that define it in other taxa. Identifying the key functions this region plays in behavior is then important for what it tells us of the division of labor in deuterostome nervous systems generally, and in the brains of chordates more specifically.

What we know of the neural circuitry and probable function of the amphioxius dien-mesencephalon comes largely from serial reconstructions of the larval CNS (see Wicht & Lacalli, 2005 for a summary). These identify the post-infundibular (=tegmental) neuropile as the principal integrative center for the animal at the stage where it first begins to swim. This accords with what is known of vertebrates, where a comparable part of the anterior brainstem, including structures in the basal diencephalon and midbrain, has a long evolutionary history as decision-making center, especially in relation to the control of locomotory responses (Grillner, Robertson & Stephenson-James, 2013; O'Connell & Hofmann, 2011). This is also where some forms of primary consciousness are thought to reside (e.g. Barron & Klein, 2016; Mashour & Alkire, 2013; Merker, 2007), which begs the question of whether amphioxius has anything useful to tell us about the evolutionary origin of vertebrate consciousness. The purpose of this paper is to explore this question, especially in relation to the evolutionary scenario laid out by Feinberg and Mallatt (2016a,b), who postulate a close association between consciousness and the emergence of the vertebrate optic tectum as a processing center for visual input.

Consciousness, for the purposes of this review, refers to the most basic form of primary, or sensory, consciousness: subjective experiences created by the brain and characterized by specific sensations, or qualia, for each category of sensory input. Two issues are then considered. The first is that there is a plausible case to be made that midbrain-based consciousness may have evolved as part of an enhanced arousal system for predator avoidance (e.g. see Feinberg & Mallatt, 2016a, Chaps. 4 & 5), but this could have happened

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