

Review article

Conserved patterns of axogenesis in the panarthropod brain[☆]George Boyan^{*}, Leslie Williams, Yu Liu

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ABSTRACT

Neuropils in the cerebral midline of Panarthropoda exhibit a wide spectrum of neuroarchitectures – from rudimentary to highly elaborated – and which at first sight defy a unifying neuroarchitectural principle. Developmental approaches have shown that in model arthropods such as insects, conserved cellular and molecular mechanisms first establish a simple axon scaffold in the brain. However, to be adapted for adult life, this immature ground plan is transformed by a developmental process – known in the grasshopper as “fascicle switching” – in which subsets of neurons systematically redirect their growth cones at stereotypic locations across the brain midline. A topographic system of choice points along the transverse brain axis where axons decussate features in all panarthropods studied even though different modes of neurogenesis and varying degrees of neuropilar elaboration are involved. This suggests that the molecular mechanisms regulating choice point selection may be conserved. In combination with recent cladistic interpretations of arthropod phylogeny based on nuclear protein-coding sequences the data argue for this topographic decussation as having evolved early and being a conserved feature of the Panarthropoda. Differences in elaboration likely reflect both the extent to which neuropilar reorganization has progressed during development and the lifestyle of the individual organism.

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1. Introduction

Adaptive behavior requires an appropriate neuroarchitectural substrate, so that each nervous system may be considered an evolutionary adaptation to a unique set of selection pressures. In model insects such as the grasshopper *Schistocerca gregaria* and the fruitfly *Drosophila melanogaster*, for example, the protocerebrum contains a highly structured neuropil known as the central complex comprising five major modules: the protocerebral bridge (PB), fan-shaped body (FB) (also known as the central body), ellipsoid body (EB), noduli (N) and lateral accessory lobes (LAL) (Williams, 1975; Renn et al., 1999; Heinze and Homberg, 2008; el Jundi et al., 2010; Young and Armstrong, 2010a,b; Boyan and Reichert, 2011; Ito et al., 2014). The most prominent of these modules is the fan-shaped body (Strausfeld, 1976, 2012) whose neuroarchitecture in insects as diverse as the grasshopper (Fig. 1A), *Drosophila* (Fig. 1B), Coleoptera (Wegerhoff et al., 1996), Collembola (Kollmann et al., 2011), and Diplura (see Fig. 8; Böhm et al., 2012), is characterized by a stereotypic columnar organization formed by the projections

of clusters of neurons located in the pars intercerebralis region of each cerebral hemisphere. These so-called small-field neurons (Homberg, 1987, 1991; Hanesch et al., 1989; Heinze and Homberg, 2008; Young and Armstrong, 2010a,b) direct fibers initially to the protocerebral bridge, and then to the fan-shaped body via one of four bilaterally symmetrical tract systems (Fig. 1A, B). Fibers enter the fan-shaped body where they arborize in specific subregions (Ito and Awasaki, 2008; Riebli et al., 2013), and may exit to run to other modules of the central complex or to other brain regions (Fig. 1E; Williams, 1972, 1975; Ito et al., 2014).

Comparative studies, on the other hand, report a wide spectrum of neuroarchitectures – from rudimentary to highly elaborated – in the cerebral midline across the Arthropoda, and which at first sight defy a unifying neuroarchitectural principle (see Strausfeld, 2012). Nevertheless, despite such structural diversities, the underlying developmental mechanisms for generating midline neuropils may be conserved across species. A further, perhaps surprising, result to emerge from developmental studies on insects to date is that the intricate neuroarchitecture of the mature fan-shaped body is not what is initially built in the cerebral midline. Instead, conserved cellular and molecular mechanisms establish an initial orthogonal axonal scaffold in which commissural axons remain tightly bundled within their fascicles (Fig. 1C; see Reichert and Boyan, 1997; Boyan and Reichert, 2011). Subsequently, similar developmental steps

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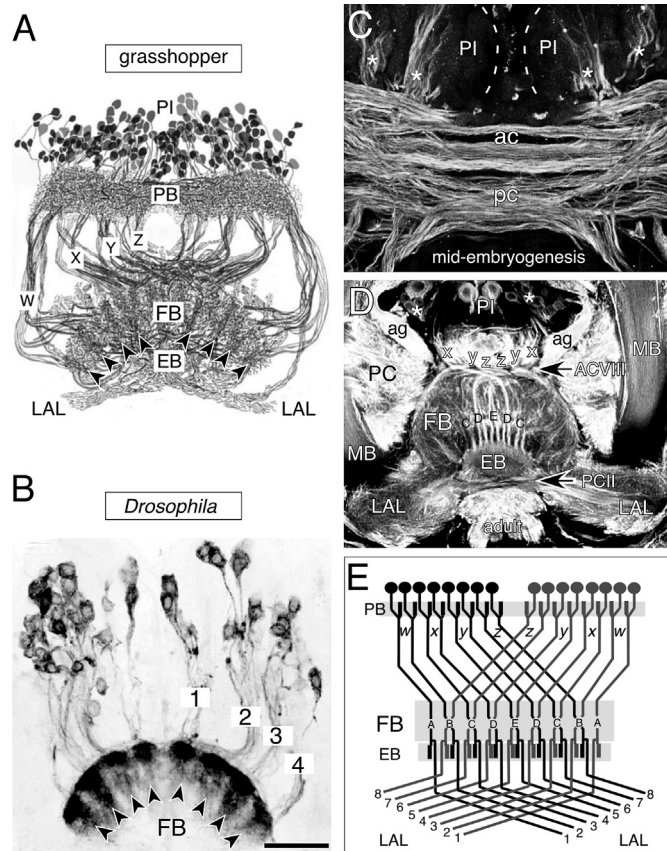


Fig. 1. The fan-shaped body (FB) in the protocerebral midline of the model insects grasshopper (A) and *Drosophila* (B). **A.** Drawing (semi-schematic) shows clusters of small-field pontine neurons from the pars intercerebralis (PI) of the adult grasshopper brain whose fibers project initially to the protocerebral bridge (PB), and then via one of four bilaterally symmetrical tract systems (w, x, y, z) to the FB, where they generate a stereotypic columnar organization (black arrowheads). **B.** Confocal image at 24 h after puparium formation following immunolabeling with *Drosophila* neuronal (Dn)-cadherin reveals four clusters of pontine neurons per hemisphere projecting fibers via four bundles (1, 2, 3, 4: terminology from Young and Armstrong, 2010b) to the FB where they generate a columnar neuroarchitecture (black arrowheads). Note the similarity to the w, x, y, z tract system of the grasshopper brain in A. **C, D.** Metamorphosis of brain neuroarchitecture in the grasshopper. **C.** Confocal image from the immature grasshopper at mid-embryogenesis following axon-specific 8B7 labeling reveals a purely commissural neuroarchitecture in which axons remain associated with their original anterior (ac) or posterior (pc) fascicles. Axonal decussation (fascicle switching) has not yet commenced. **D.** In the adult grasshopper, axon-specific 8B7 labeling reveals a highly elaborated neuroarchitecture dominated by a fan-shaped body (FB) with its stereotypic 9 columnar organization (columns C, D, E, D, C are visible in this section), and an ellipsoid body (EB), both flanked by the mushroom bodies (MB). The FB is delimited anteriorly (ACVIII) and posteriorly (PCII) by commissural fascicles (terminology is from Boyan et al., 1993). **E.** Schematic summarizes the basic neuroarchitecture of the adult central complex of the grasshopper. Eight symmetrical cell clusters in the pars intercerebralis of each brain hemisphere (deriving from the four embryonic W, X, Y, Z neuroblasts respectively, not shown) direct neurites to the protocerebral bridge (PB) where they arborize, and then axons to the FB via the bilateral w, x, y, z tracts. En route across the brain midline these bilateral projections form a topographic system of chiasmata. Within the FB, 9 fiber columns are present each formed by unique combinations of projections from the bilateral w, x, y, z tract system (A, w; B, w/z; C, x/z; D, x/y; E, y/y). The axons then traverse the ellipsoid body (EB) and may cross the midline again to project to other modules of the central complex such as the lateral accessory lobes (LAL). Other abbreviations: ag, antennoglomerular tract; AL, antennal lobe; LAL, lateral accessory lobe; PC, protocerebrum. Scale bar represents: 130 μ m in A; 35 μ m in B, C; 170 μ m in D. Panels A, C, D modified from Boyan and Williams (2011) with permission; panel B modified from Young and Armstrong (2010b) with permission; panel E modified from Williams (1975) with permission.

reshape this rudimentary neuroarchitecture to generate the highly structured, modular, neuropil adapted for adult life known as the central complex (Fig. 1D,E; Strausfeld, 1976, 2009, 2012; Boyan and Reichert, 2011).

The transformation of this initial orthogonal ground plan into the mature chiasmatal/columnar neuroarchitecture involves a topographic decussation of axons (known as “fascicle switching” in the grasshopper), in which homologous clusters of neurons from each protocerebral hemisphere redirect their axonal growth cones at stereotypic locations across the cerebral midline (Boyan et al., 2008a; Young and Armstrong, 2010a,b). This reorganization is evidence that developmental mechanisms can transform neuroarchitectures to fit a changing lifestyle even within the lifespan of an individual organism (Bullock and Horridge, 1965; Levine, 1984; Boyan and Ball, 1993; Lawrence, 1993; Sanes et al., 2012), and may also be evolutionarily conserved (Strausfeld and Hirth, 2013).

Our aim in this review is to examine whether the pattern of axogenesis reported for insects represents a conserved principle for organizing the cerebral midline throughout the panarthropods (arthropods plus onychophorans, see Strausfeld, 2012). To this end, we first review our knowledge of the basic patterns of neurogenesis and axogenesis where these have been most extensively studied in the cerebral midline, namely in the grasshopper and *Drosophila*, and then extrapolate to other panarthropods. We show that although the mode of generating neurons can differ significantly across the panarthropods – individual precursor cells in insects, crustaceans and onychophorans, as opposed to invaginated proliferative cell clusters in chelicerates and myriapods – the molecular mechanisms regulating precursor selection are conserved in arthropods as phylogenetically distant as insects and chelicerates, and we speculate such mechanisms may extend to other panarthropods as well. Equally, a comparison of cerebral neuroarchitectures shows that a basically similar topographic redirection of axon projections also features in all panarthropods examined despite the different modes of neurogenesis and varying degrees of neuropil elaboration. In combination with cladistic analyses based on nuclear protein-coding sequences, this mode of axogenesis appears to have evolved early, and represents a conserved feature of the Panarthropoda. We suggest that differences in elaboration of this neuropil most likely reflect both the extent to which axonal reorganization has progressed during development and the lifestyle of the individual organism.

2. Building cerebral midline neuroarchitecture: basic principles from the insect

2.1. Ontogeny: stem cells and lineages

Topologically, the central complex belongs to the protocerebral neuromere of the brain, and in both the grasshopper and *Drosophila*, the protocerebrum is generated by approximately 100 bilaterally symmetrical pairs of stem cells called neuroblasts (NBs), each of which is individually specified (Reichert and Boyan, 1997; Boyan and Reichert, 2011). This specification is determined by a combination of positional information, temporal cues, and combinatorial cues originating from the suite of developmental control genes expressed by each progenitor (Zacharias et al., 1993; Younossi-Hartenstein et al., 1996, 1997; Boyan and Williams, 1997; Skeath and Thor, 2003; Urbach and Technau, 2003; Urbach et al., 2003a,b; Urbach and Technau, 2004; Williams et al., 2005; Technau et al., 2006; Doe, 2008; Kao and Lee, 2010). Cellular analyses in the grasshopper show that four of the 100 identified NBs in each hemisphere play a key role in central body development in that their progeny establish the basic columnar organization of its neuropil. These four NBs, termed W, X, Y, Z, each generate a lineage of neurons which contribute fibers to substructures of the central complex via the so-called w, x, y, z brain tracts (c.f. Fig. 1A,E; Boyan and Williams, 1997; Williams et al., 2005). Genetic analysis reveals that a similar set of NBs (termed DM) is found in each hemisphere

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