system was independently lost/modified many times. The differences between vertebrates and *Drosophila* in the upstream modulators of dorsoventral transcription factors and in their functional integration[32,38] should thus be regarded as a case of developmental system drift[39] over large phylogenetic distances. Alternatively, and more parsimoniously, these differences may indicate that the commonalities in dorsoventral nerve cord organization between vertebrates, arthropods, and some annelids evolved convergently (Fig. 6b and Extended Data Fig. 10c). The similar staggered expression domains of dorsoventral transcription factors in these three lineages, together with those uncovered by our study (Figs 3 and 4), might reflect the existence of ancient ectodermal gene regulatory sub-modules[16,37,40,41] that got repeatedly assembled for the patterning of bilaterian nerve cords and neuronal cell type specification. Therefore, advancing our understanding of CNS evolution largely relies on functionally identifying the developmental implications of the anteroposterior and dorsoventral patterning systems in diverse bilaterians, before they can be used to homologize particular morphological structures and cell types[5,42].

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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