

Decussation as an axial twist: A Comment on Kinsbourne (2013)

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Abstract:

One of the great mysteries of the brain, which has puzzled all-time students of brain form and function is the contralateral organization of the forebrain, and the crossings of its major afferent and efferent connections. As a novel explanation, two recent studies have proposed that the rostral part of the head, including the forebrain, is rotated by 180 degrees with respect to the rest of the body (de Lussanet and Osse, 2012, *Animal Biology* 62, 193–216; Kinsbourne, 2013, *Neuropsychology* 27, 511–515). Kinsbourne proposes one 180-degree turn while we consider the 180 degrees being the result of two 90-degree turns in opposite directions. We discuss the similarities and differences between the two hypotheses.

Keywords:

body axis, embryogenesis, brain evolution, brain asymmetry, decussation, chiasm, situs inversus

Comment:

Recently, two studies have independently proposed similar hypotheses to explain the extensive decussations that exist between the forebrain and the rest of the nervous system of all vertebrates as an axial twist (de Lussanet and Osse, 2012; Kinsbourne, 2013). Both hypotheses propose this twist to be a „spandrel“, an inevitable byproduct of another evolutionary event, in the sense of Gould (1997). In doing so, these two studies contributed to a discourse on one of the grand mysteries of the vertebrate body plan which was first initiated by Ramón y Cajal (1899), whose view has turned out to be unsatisfactory. Cajal proposed that by the chiasm, the left and right eyes together produced a consistent image of the outside world in the brain. The major objections are: the two hemispheres of the brain are only connected by the small posterior and anterior commissures (and in mammals additionally by the corpus callosum), and the eye movements of lateral-eyed vertebrates are not coupled (de Lussanet and Osse, 2012). Moreover, Ramón y Cajal's central idea that the crossing brings the medial edges of the visual field in physical vicinity is wrong, at least in the mammalian visual cortex, where the lateral visual periphery is projected on the medial side of the retinal map in each hemisphere.

According to Kinsbourne (2013; he published an early form of his ideas already in 1978) the forebrain and the anterior head region (including the mouth) is turned by 180° about a rostro-caudal axis (Fig. 1A), as a byproduct of the dorso-ventral inversion of the body (compare the earthworm-to-vertebrate construction of Geoffroy-Saint-Hilaire, 1822). The dorso-ventral inversion hypothesis has seen renewed interest since the discovery of genetic dorso-ventral patterning mechanisms (Arendt and Nübler-Jung, 1994; Holley et al., 1995).

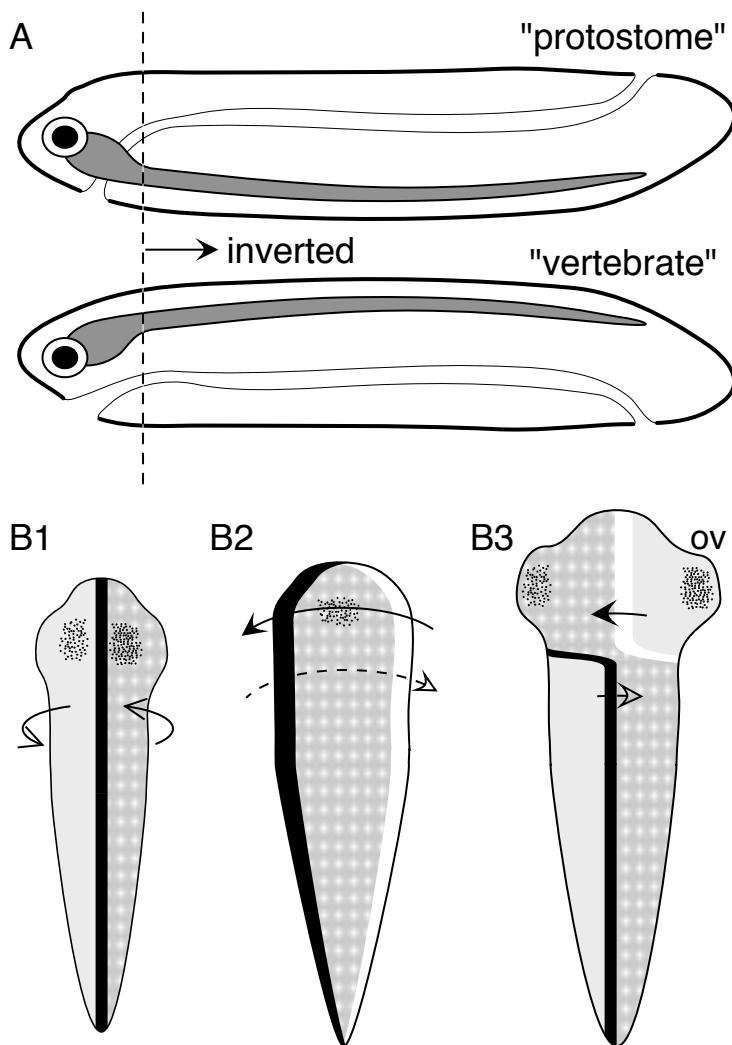


Figure 1. Panel A shows a schema (by us) of the „somatic twist model“ of Kinsbourne (2013). Kinsbourne’s model is based on the dorso-ventral inversion hypothesis with the additional assumption that the rostral head region is not inverted and therefore twisted by 180 degrees with respect to the rest of the body. Panel B shows a schema of the early developmental deformations of our axial twist hypothesis (de Lussanet & Osse, 2012). The embryo is viewed from above, with rostral up. Black zone: dorsal; white zone: ventral; spotted: right side; dotted: prospective eye region; ov: optic vesicle. The embryo turns on its left side, as indicated by stick-arrows (B1). Bilateral symmetry is restored by further 90° leftward turn of the rostral head region (filled arrows) and 90° opposite (dashed arrows) turn of the body (B2). Consequently, the rostral region is inverted with respect to the rest of the body (B3). Panel B was reproduced with permission from (de Lussanet & Osse, 2012).

Our axial twist hypothesis (de Lussanet and Osse, 2012) can be summarized as follows (Figure 1B). We proposed that the vertebrate gastrula is oriented on its left side. Just prior to neurulation the forebrain-eye region turns 90° clockwise (when facing the embryo). Subsequently, a 90° anti-clockwise turn sweeps over the rest of the body starting from the mid-brain region in a caudal direction, but sparing the heart and other inner organs. Both turns are known in the literature; the latter is very well-known. The sum of the clockwise and anti-clockwise turns makes that the forebrain, eyes and olfactory organ are rotated by 180° along the rostrocaudal axis.

The two hypotheses share considerable explanatory potential. Both can explain the presence of a ventral optic chiasm and also the unusual representation of visual information in the forebrain of cartilaginous fishes such as the shark (Ebbesson and Schroeder, 1971). In them, the visual pathway decussates twice: at first in the optic chiasm, and then again, after passing the optic tectum, in the tecto-thalamic decussation. Further, both models predict that olfactory tract should be uncrossed. In addition, both hypotheses explain the decussation of the trochlear nerve, and why the cerebellar hemispheres represent the ipsilateral bodyside.

On the other hand, our model is the only one that explains the asymmetric location of the heart and gastrointestinal tract, as the only part of the body that has no part of the twist because there has been no evolutionary pressure for bilateral symmetry on these organs. Our model explains

why the brain is turned by 90 degrees in some developmental disorders such as in holoprosencephaly and in janiceps twins.

Except for these internal organs, the predictions of the two hypotheses are anatomically hardly distinguishable. Also from a genetic perspective the two models are similar, because both predict that the dorsoventral and lateral body axes should be inverted in the anterior head region as compared to the rest of the body.

A shared weakness of both hypotheses is that they explain only part of the decussations in the central nervous system and that not all neurons decussate in the optic chiasm (Larsson, 2011). For example, neurons cross the midline of the forebrain through the corpus callosum and the anterior and posterior commissures, but also in every other part of the nervous system, such as, for example, the Müller and Mauthner cells of the hindbrain (Ebbesson, 1980). Such cells typically cross the midline in the same segment where they originate, whereas the two twist hypotheses specifically address decussations of connections between the forebrain and the rest of the nervous system (and thus typically decussate in a segment which is different from their origination). Another shared weakness is that in both hypotheses the decussations are a „spandrel“ of hypothetical evolutionary adaptations: the hypothetical dorso-ventral inversion (Kinsbourne) and a side-turn (de Lussanet & Osse).

In our opinion a side-turn is more likely than a full dorsoventral inversion, from an evolutionary perspective because it presents a clear parallel to the asymmetric development in clades that share a common ancestry with vertebrates such as cephalochordates, tunicates and echinoderms (de Lussanet, 2011).

Given the weaknesses explained above we have looked for additional supported by developmental evidence. Indeed we did find evidence for a clockwise turn in the anterior head region and an anti-clockwise turn in the rest of the body (except the heart and gastrointestinal system) in published literature for both an amniote (the chick) and a teleost (the zebra fish) (de Lussanet and Osse, 2012).

As a final remark, we would like to mention that we, too, have briefly discussed the dorso-ventral inversion theory in our original paper. There we came to the conclusion that our hypothesis could be compatible with the dorso-ventral inversion hypothesis, depending on the location of the mouth. Assuming that the mouth will appear in a location that turns with the anterior part of the head the two hypotheses would be compatible. However, given that the vertebrate mouth develops very late, it cannot be decided at present whether they really are.

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