

THEORETICAL REVIEW

Somatic Twist: A Model for the Evolution of Decussation

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Objective: In the chordate and vertebrate central nervous system, sensory and motor nerve tracts cross from one side to the other as they connect the brain with sensory receptors and motor neurons. These “decussations,” crossings in the form of an X, relate each side of the brain to the opposite side of the body. The protochordates derive from an invertebrate ancestor, but no such contralateral arrangement occurs in any invertebrate phylum. No adaptive benefit of decussation has been established. What might explain the evolution of decussation? **Method:** A brief review of relevant features of comparative morphology of invertebrates, chordates and vertebrates leads to an explanatory model of decussation. **Result:** A “somatic twist model” of invertebrate-vertebrate transition accounts for decussations as byproducts of a more momentous change; the relocation of the neuraxis from the ventral to the dorsal aspect of the body. Evidence is presented that this inversion proceeded by means of a twisting of the body 180 degrees on its axis just behind its anterior pole. This rotation aligned the neuraxis with the dorsal head ganglia and brain and by twisting the nerve tracts it brought decussation in its wake. **Conclusion:** Decussation evolved as a byproduct of a genetically determined partial inversion of the body plan, which resulted in a 180 degree rotation posterior to the brain and oropharynx.

Keywords: decussation, somatic-twist, invertebrate, chordate, vertebrate

The smallest worm will turn.

—William Shakespeare, *Henry VI* (Part 3)

Bilaterally symmetrical animals (Bilateria) have paired nerve cords or a bisymmetric spinal cord with bilaterally parallel tracts running in the anterior-posterior direction. Only in chordates and vertebrates do the sensory and motor tracts decussate, so that sensory input and motor commands engage the left side of the body with the right brain and vice versa. Hippocrates (460–380 BC) was aware that injury to one side of the human brain results in convulsion or paralysis on the opposite side. This anatomical design characteristic is of fundamental significance to the science of neuropsychology, as witnessed by the vast literature on laterality in animals and man. Yet the protochordates, the ancestors of the vertebrate subphylum, have invertebrate ancestry and invertebrates have ipsilateral sensorimotor control. How did decussation arise in these tiny worm-like inhabitants of shallow waters, perhaps 600 million years ago, and why?

Adaptations

When a novel structure appears in evolution, the first thought is that it was selected on account of an adaptive advantage. The challenge in uncovering an adaptive advantage for introducing

decussation into longitudinal nerve tracts is to show how it would plausibly apply to the 50,000 species in the chordate phylum, and, as importantly, how it would not apply to the approximately 35 other phyla with their far in excess of one million species. Many hypothetical adaptive advantages for decussation have been proposed. They range from simplistic (decussation helps bind the brain together) to more elaborate, summarized by Vulliamoz, Raineteau and Jabaudon (2005), who offer an up-to-date discussion of the “teleology of midline crossing” (p. 8). They evaluate and reject Ramon y Cajal’s proposal that the optic fibers cross at the chiasm to maintain continuity between the two visual fields at the midline. Braitenberg (1965, pp. 210–212) offers a more extensive refutation of Cajal’s model. A case report of a patient with only ipsilateral optic projections finds him unimpaired with regard the sweep and continuity of his visual field (Victor, Apkarian, Hirsch, et al., 2000), counter to prediction from Cajal’s model. However, he is unable to perceive binocular depth.

Sarnat and Netsky (1974, pp. 67–71) suggested that the decussation of motor control was an adaptation in support of the defensive coiling reflex as observed in amphioxus, providing a direct pathway for animals to withdraw the threatened side. However, coiling reflexes are frequently found among invertebrate species, without reports of decussation (Kavaliers, 1988). On similar lines, Vulliamoz, Raineteau and Jabaudon (2005) suggest that decussation facilitates escape behavior in limbed vertebrates, by enabling instant contraction of the limbs ipsilateral to the threat, and therefore controlled by the opposite hemisphere. However, vertebrates without limbs have the same body plan as those with limbs.

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None of the “teleological” models have gained general acceptance. However, evolutionary change is not always a result of adaptive advantage. Perhaps the search for an adaptive benefit of decussation is a blind alley. A structural design characteristic may survive and be widely instantiated for reasons other than any specific adaptive advantage it might bestow.

Byproduct

Rather than offering any adaptive advantage, did decussation arise as a structural byproduct of a far more general bodily rearrangement in the invertebrate-vertebrate transition? The neuraxis of invertebrates such as arthropods and annelids originates at the leading end of the body in a dorsally located ganglionic mass or a more complex brain, which is dorsal to the oropharynx, but then sweeps back along the ventral aspect of the body for the length of the animal (Nieuwenhuys, 1964, Figure 1). The paired nerve cords are of ladder type, a double chain of longitudinal strands of connected ganglia, with horizontal interconnections (Weichert, 1958, p. 7).

In contrast, the chordate and vertebrate neuraxis projects along the dorsal part of the body, dorsal to the notochord, and in direct line with the brain. The brain is dorsal to the oropharynx in vertebrates and invertebrates alike (Weichert, 1958, p. 8; Figure 1). This ventral to dorsal inversion of structure during the transition is not, however, an isolated change. It is related to the concurrent appearance in the earliest chordates (protochordates such as tunicates, acorn worms and amphioxus) of a notochord, a pliant

rod-like structure, the precursor of the vertebral column (Weichert, 1958, p. 7). Features such as these may have bestowed a sufficient adaptive advantage for the vertebrate body plan to be conserved.

Dorsoventral Inversion

Nearly two hundred years ago, E. Geoffroy St. Hilaire, a French naturalist, suggested that the ventral half of arthropods is homologous with the dorsal half of vertebrates (St. Hilaire, 1822). He observed that when he turned a crayfish upside down, the neuraxis was now above the digestive tract, which in turn was above the heart, as they are in chordates and vertebrates. His idea that dorsoventral inversion had occurred at the invertebrate to vertebrate transition was long discounted, perhaps because inversion seemed too abrupt and not gradually incremental as Darwinian adaptations were thought to be. But since Waddington's (1974) catastrophe theory of evolution and Gould's notion of evolution by punctuated equilibrium gained currency (Gould & Eldredge, 1993), current thinking has become more amenable to rapid evolutionary change, as is implied in St. Hilaire's dorsolateral inversion model and also in the idea of somatic twist. Indeed, referring to St. Hilaire's inversion hypothesis, Lacalli (2010) wrote, “an idea considered bizarre little more than a decade ago is now both widely accepted and a fruitful source of insights into past evolutionary events.” Arendt and Nubler-Jung (1999) and Holland (2009) among many others, review convincing evidence from molecular genetics that finds the same highly conserved genetic organizers of spatial relations in the body plan in invertebrate and vertebrate species. This work revealed homology between ventral structures in the invertebrates and corresponding structures in the chordate, which however were dorsally located. Genetic markers that indicate “dorsal” in the chordate indicate “ventral” in the invertebrate. These highly conserved patterning genes reveal homology between the vertebrate dorsum and the invertebrate ventrum, as St. Hilaire suggested. They are thought to indicate a common ancestral urbilaterian brain.

Two additional morphological distinctions could be proffered as evidence for dorsoventral inversion. One is neurological and the other is cardiovascular.

In the spinal cord of amphioxus (lancelet), a cephalochordate that is taken to be crucial to the riddle of invertebrate-vertebrate transition, there is “a dorsal, chiefly sensory region and a ventral predominantly motor area” (Nieuwenhuys, 1964). In the neuraxis of invertebrates, these relations are reverse. What remains constant between phyla is the relation of these tracts to the animal's body surface. The sensory tracts are more superficial, the motor tracts deeper, as would be found if the body rotated as a whole. Of course these simple relationships become complicated by massive subsequent additional complexity in the course of vertebrate evolution. Yet the dorsal sensory versus ventral motor arrangement is still vividly obvious in the mammalian cerebrum, with sensory modalities in dorsal areas and motor planning in frontal areas.

Evidence in support of inversion of the body also derives from the direction in which the blood circulates. In typical invertebrates a pulsating vascular structure, or heart, is situated on the dorsal side of the body. Blood is pumped toward the ventral aspect of the body, flows in a posterior direction, and finally returns to the heart by a dorsal route. A well-characterized instance is found in the giant earthworm (Johansen & Martin, 1965). The main distributing

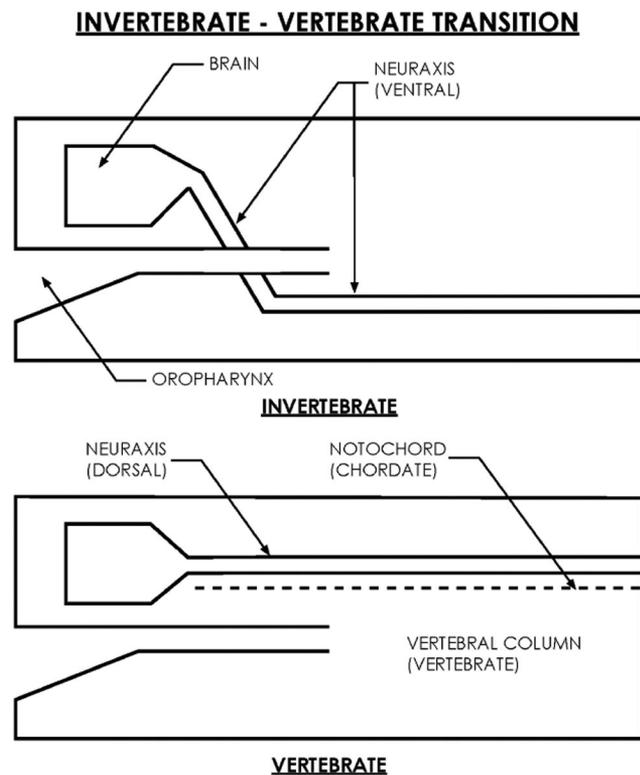


Figure 1. Schematic representations of the contrasting course of the neuraxis in invertebrates and in vertebrates.

vessel is located ventrally, and the main collecting vessel is dorsal. Conversely, the chordate heart is on the ventral side of the body. Blood is propelled to the dorsal side. It then courses in a posterior direction and returns to the heart through large veins which are ventral in position (Weichert, 1958, p. 10). This reversal of direction of flow between the invertebrate and the chordate is consistent with dorsoventral somatic inversion.

Somatic Twist

Dorsoventral inversion does not explain how decussation arose, and St. Hilaire and his recent supporters have not considered decussation as being part of the inversion process. They focused their attention on the body of the animals, but not their anterior ends. A complete dorsoventral inversion would require that the chordate and the vertebrate brain is stationed ventral to the oropharynx, which has not been reported. Lacalli (2010) did recognize the problem of a hypothetically ventral brain. He postulated that after the inversion the mouth takes a separate corrective trip back from a postinversion dorsal location to its ultimate chordate/vertebrate ventral location below the brain.

A more parsimonious interpretation would consider the anterior end of both the ancestral invertebrate and the vertebrate body to be an invariant anchor for an inversion of the rest of the body in back. The inversion would then be not of the organism as a whole, but of the bulk of the body situated behind the leading end, and specifically behind the brain or its rostral end, and the oropharynx. The animal's body would have twisted 180 degrees relative to its leading end, a "somatic twist."

Somatic twist explains decussation. When lateralized nerve tracts are twisted, this diverts them from one side of the body to the opposite side. It also reverses the locations of the individual fibers relative to the tract as a whole. Both of these rearrangements are seen in ascending and descending tracts of the vertebrate nervous system. Thus fibers emanating from one extreme side of a tract proximally connect with the extreme opposite side distally (see Figure 2).

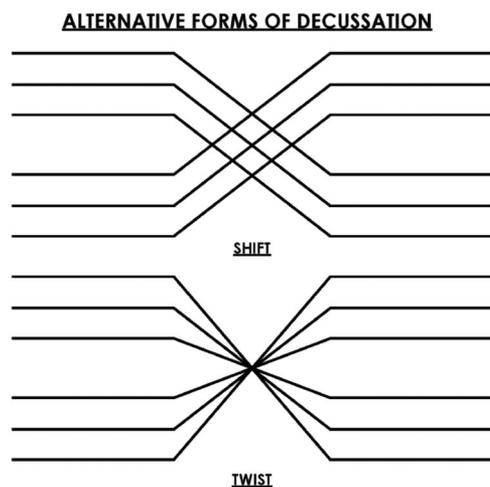


Figure 2. Decussation could be implemented in two alternative ways as the parallel nerve fibers either shift laterally or twist around each other.

Decussation can already be identified in amphioxus. The sensory cells of Rohde, giving rise to decussating giant fibers, project between the rostral and the caudal segments of the spinal cord. They establish a pattern for the decussation of longitudinal nerve tracts that has been conserved in vertebrates. In all vertebrates these tracts in the spinal cord decussate in a commissure ventral to the central canal, as they do in amphioxus. "In evolution, amphioxus or a similar ancestor of man had the first decussation in the central nervous system" (Sarnat & Netsky, 1974, p. 64). Interestingly, in the larva the axons of the most anterior giant cells do not decussate but course posteriorly on the same side (Bone, 1960).

The optic chiasm offers an example in which crossed nerve tracts twist, rather than simply shift sideward in direction. The incoming fibers of the optic nerve decussate in the optic chiasm. They don't simply shift across to the other side. They twist around 180 degrees so that the most temporal fibers from the retina of one eyeball travel to the most lateral section of the opposite visual cortex. Mathematically, the rotation matrix changes all x coordinates to $-x$ and all y coordinates to $-y$; $R(x, y) = (-x, -y)$.

The genetic control of the relative position of body parts by patterning genes is separate from the specification of the parts. Rotations of 180 degrees are not without precedent in the ontogeny of some species. The terminal two or three body segments of males of some subspecies of Diptera rotate, bringing their copulatory equipment into adult position. Crampton (1941) reported a permanent inversion of the ninth segment (which is rotated about the long axis through 180 degrees) in male Culicidae and other Diptera. An elaborate process of 180-degree rotation occurs in embryonic snails (Pseudobranchia). Mutations in *Drosophila* have been documented that result in bodies twisted a variable number of degrees, clockwise or counter clockwise, including complete inversion (Lindsley & Zimm, 1992).

At what level of the central nervous system might the twist have occurred? A level anterior to which there would be no crossover of tracts. One sensory structure does project to ipsilateral higher centers. The olfactory nerve, the first and most anterior of the cranial nerves and presumably proximal to the twist, is the only cranial nerve that does not decussate. Already in amphioxus, Churcher and Taylor (2009) reported odorant receptors that feed ipsilaterally into the extreme anterior end of the "brain." The paradoxical ipsilateral connections of the olfactory nerves have not previously been explained.

Almost all the ascending and descending tracts in vertebrates evolved well after the presumptive somatic twist, the corticospinal tracts latest of all. Although amphioxus has an assortment of cells that sense mechanical perturbation and light, it lacks special senses other than rudimentary olfaction as noted above. Nonetheless, the vertebrate tracts conform to the earlier established crossed body plan. Sarnat and Netsky (2002, p. 249) explained why later developing sensory and motor systems conformed to the crossed body plan. "As the vertebrate brain evolved the decussating interneuron of Amphioxus was reproduced in progressively more rostrally evolving structures, exemplified in descending pathways as the olivospinal, vestibulospinal, tectospinal and finally the corticospinal tracts. Once the crossed pattern was established by an ancestral amphioxus, additional new neurological pathways were obliged to follow this template so that signals with confused laterality would not be sent."

The effort to discern the body plan of the ancestral chordate has not resulted in the discovery of a living organism that fits specifications. This is hardly surprising because some 600 million years afford ample time for further selection pressures to modify the features of any then living species. The same would apply to the search for the original twisted ancestor as proposed in this discussion. Although decussation has been impressively conserved, and the twist is proposed to have occurred at a specific segmental level, there is no one level in contemporary protochordate or vertebrate brains at which all the decussations are to be found. Whereas the corticospinal tracts cross in the brainstem, the pain fibers cross where they enter the spinal cord and the nerves that transmit information as to vibration, travel some segments toward the brain before they cross. Since chordates first appeared, subsequently evolved momentous central nervous system innovations in the much larger vertebrate embryo may have distorted the relative spatial relationships of existing decussations. When the rest of the cranial nerves evolved below twist level in the course of phylogeny, they aligned with the existing contralateral blueprint for sensorimotor functioning. However, there is no known corresponding adaptive constraint for the crossing to occur at the same segmental level as the original twist. As long as the result was contralateral control, the exact level of the crossing in the case of each individual tract would presumably be subject to as yet unknown local factors.

In contrast, later developing projections that serve the axial musculature might not need to align with the existing sensorimotor lateralities. Examples may be the uncrossed reticulospinal and vestibulospinal tracts, which largely assist in the control of axial motor structures that do not align with the sensorimotor systems for detecting and responding to external events and therefore are not constrained by the decussating body plan. The ipsilateral components of the optic chiasm are also a product of much more recent evolution. "Crossing is complete in all vertebrates except in those mammals having binocular vision" (Weichert, 1958, p. 595, Figure 13.17). In the course of the development of the optic nerve some of the otherwise crossing fibers are chemically steered in an ipsilateral direction in animals that acquire three-dimensional binocular vision (Petros, Rebsam, & Mason, 2008).

Have there been alternative accounts of the origin of decussation by somatic twist? I first presented the concept of decussation by somatic twist to a meeting of the New York Academy of Sciences in 1976. I included a brief outline in a chapter in my edited book on the Asymmetrical Function of the Brain (Kinsbourne, 1978, p. 554–557). Since then I have presented this idea in invited lectures but not until now in a formal article. During this long period of time I am unaware of any article that features a dorsoventral inversion with somatic twist. The closest in concept are Lussanet, et al. (2012), who postulate a 90-degree turn of the head to the left in a common ancestor of vertebrates, with compensatory migrations that restored body symmetry, such that the forebrain becomes inverted with respect to the rest of the nervous system. Although it invokes an axial twist, this model does not propose a turn of 180 degrees but of 90 degrees, and it does not relate the twist to the migration of the neuraxis to a dorsal from an ancestral ventral position, with successive formation of notochord and vertebral column during the invertebrate-vertebrate transition. Instead it locates the twist in a vertebrate rather than a protochordate ancestor.

The concept of somatic twist offers potentially testable predictions. It regards the axial twist as integral to the formation of a dorsal neuraxis, and therefore places it in an ancestor of protochordates, not vertebrates. It regards decussation and the somatic twist as intrinsically linked. Decussation is taken to be a by-product of another quite different structural modification. Because the twist necessarily results in decussation of tracts that course through the twisted area, no organism should come to light in which the neuraxis is dorsal but decussation is absent. The main direction of blood flow in the caudal direction would also be predicted to be dorsal to ventral in species in which the chief nerve tracts decussate and ventral to dorsal in species in which they do not decussate.

Like inversion, the concept of twist implies homologies that could be identified by molecular markers, as was done to validate the inversion in the first place. Highly conserved Hox gene clusters determine the pattern of successive regions along the anterior-posterior axis of the bodies of invertebrates and vertebrates alike (Shankland & Seaver, 2000). It is intriguing that the extreme anterior region of the amphioxus embryo relies on distinct patterning genes (Otx genes) and is partitioned from the gene clusters that organize the rest of the body at the posterior end of the first somite. The first somite contains the cerebral vesicles (Wada & Satoh, 2001), which develop into the prosencephalon or forebrain (Jacobson, 1988). So theoretically, a modification of the main pattern of Hox gene activity might leave the Otx cluster in charge of the anterior end (head and brain) unaffected, resulting in the hypothesized twisted end state. Gene knockout, now feasible, might offer a critical test for the hypothesized separate genetic control of the anterior end and the rest of the animal body plan and the predicted effects on the presence or absence of decussation.

The concept that a prominent structural feature such as decussation was not a specific adaptation unique to the chordate phylum, but rather a structural feature that arose in the course of an unrelated adaptation, the ventral-dorsal twist, places it among phenomena that Gould has assembled under the term "spandrel." This is "the class of forms and spaces that arise as necessary byproducts of another decision in design, and not as adaptations for direct utility in themselves" (Gould, 1997, p. 10750). Precisely because the somatic twist is presented here as a spandrel, its persistence in chordate and vertebrate species would be attributable to the adaptive advantage of the architectural change in body plan in the wake of which it occurred.

What might have been the adaptive advantage of having a dorsal notochord or backbone? In contrast to the superficial exoskeletons of some invertebrates, the vertebral column is an endoskeleton, which provides protection for the spinal cord and internal organs, lends support to the body, and being jointed enables movement of the trunk. Its precursor, the flexible cartilaginous notochord, is also closely related to the neuraxis, which runs in parallel just dorsally. Further discussion would be beyond the scope of this article.

Decussation has been presented as a consequence of the rotation of part of the body around its anteroposterior structural axis, resulting in a body plan that has passed down from its protochordate origins to the most elaborate known vertebrate nervous systems. The rotation is integral to the development of an interior endoskeleton, as distinct from the exoskeleton of many invertebrates. The twisted body plan, and hence decussation, applies to protochordates and vertebrates and only to them precisely because

only they have a notochord or a vertebral column. So the restriction of a decussating body plan to one phylum is explained in the simplest imaginable way, in terms of the very defining characteristics of the chordate phylum.

The somatic twist model can be the answer both to how decussation happened and why it happened. If nature had intentions, decussation would have been considered an unintended consequence.

The worm did turn. It turned on itself.

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