mechanism of Ross. Whether products from chemical reactions at high pressures in Uranus or Neptune actually find their way into the observable atmosphere depends on the existence of deep-seated circulation patterns at the base of the hydrogen atmosphere and in the upper "ice" layer. Uranus is considerably less active than Neptune both from the point of view of atmospheric dynamics and interior heat flow. A possible diagnostic of communication between the atmosphere and the "ice" layer is the atmospheric abundance of deuterium relative to hydrogen, D/H. In the primordial icy objects in the outer solar system and in Earth's oceans, the D/H ratio is enhanced by nearly one order of magnitude relative to the primordial solar

DEVELOPMENT

Left-Right Asymmetry

Elizabeth J. Robertson

On the surface, the left and right sides of our bodies seem perfectly identical. But appearances can be misleading. Closer inspection reveals that all vertebrates exhibit left-right (L-R) asymmetry in the positions of their visceral organs. A striking example is provided by the heart, which invariantly loops to the right side. The molecular controls of this process are just coming into view; the latest player is reported on page 1301 of this issue (1).

Elegant experiments in the chick (2) have revealed that during L-R axis formation a number of signaling molecules are transiently expressed on only one side of the emerging midline of the embryo-including an activin receptor (ActRII), sonic hedgehog (Shh), and the transforming growth factor- β (TGF- β) family member nodal (see figure). This asymmetric pattern of gene expression precedes any tangible evidence of morphological L-R asymmetry. The very earliest signal appears to be mediated by ActRII positioned along the right side of the primitive streak shortly after the onset of gastrulation. This inductive cue is then relayed to lateral plate mesoderm cells as they migrate anteriorly from their origins in the streak and is reinforced by Shh and nodal expressed on the left side of the node. A few hours later, nodal becomes selectively expressed in a broad stripe of lateral plate mesoderm on the left side of the body axis. The primitive heart tube then begins its program of looping and bends to the right. A similar rightward rotation of the entire body axis closely follows.

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In this issue, Isaac and colleagues report that cSnR (for Snail-related), a new member of the Snail family of zinc finger proteins (1), is expressed in lateral plate mesoderm cells on the right side of the chick embryo, in a domain that roughly mirrors that of nodal on the left. Moreover, specific antisense oligonucleotides can down-regulate cSnR expression and randomize the direction of heart looping and axial rotation. Interestingly, this manipulation does not perturb nodal expression, indicating that cSnR acts downstream of nodal.

composition (6). One expects that D/H in

the Uranus and Neptune "ice" layers would

also be enhanced by this factor, so exchange

of hydrogen between the atmosphere and

interior would lead to some enhancement of

D/H in the atmosphere (7). Recent measure-

ments of D/H give values lower than the

predicted enhancement, suggesting incom-

plete communication between the atmo-

sphere and interior, particularly in Uranus.

dances in the atmospheres of Uranus and

Neptune derives from the extended Voyager

2 mission and from Earth-based and orbiting

observatories. In the case of Jupiter, compari-

sons between results from remote-sensing

data and in situ data from the Galileo probe

Our knowledge about chemical abun-

Does the same L-R pathway operate in other vertebrates? Nodal homologs are asymmetrically expressed in mouse (3, 4) and Xenopus (4). As in chick, nodal expression is caution us that abundances obtained from remote sensing must be interpreted with care and that entry probes will probably be needed for definitive determinations of atmospheric abundances in the giant planets.

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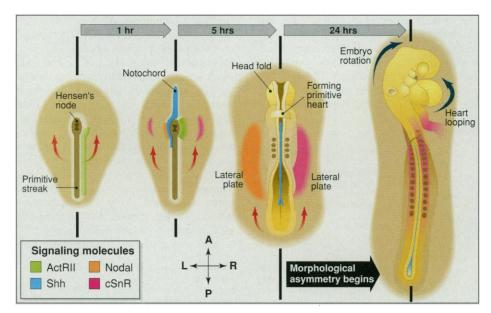
strictly confined to mesoderm populations on the prospective left side of the embryo. In both mouse and chick, alteration of the sidedness of nodal expression is sufficient to change both the direction of heart looping and embryonic turning (1, 3, 4). What could cSnR contribute to these morphogenetic processes? Perhaps nodal represses cSnR expression on the left side of the axis. Indeed, Isaac et al. show that perturbing the initial L-R cue with soluble activin randomizes expression of both nodal and cSnR in later stage chick embryos (2). Mutually exclusive patterns of nodal and cSnR expression could potentially activate distinct sets of downstream target genes. Hopefully these missing pieces of the L-R puzzle can soon be coaxed into view.

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