women. But subsequently this group reported that there was no sex difference in the numbers of neurons in the human SDN-POA until ten years of age⁹.

Thus there is ample room for early experiences, including the very different social stimuli presented to boys and girls, to cause the sex difference found in the adult SDN-POA. Similarly, we do not know how INAH-3 develops in humans, so it is not clear whether this sexual dimorphism is a cause or an effect of human sexual differentiation. Neither do we know whether some men having a small INAH-3 at birth are therefore born gay or, more correctly, born to become gay as adults. Only a sexual dimorphism found in newborn or fetal humans could safely be described as unrelated to social stimulation.

At present, these brain regions can only be measured post mortem. Until technology enables us to measure them

DEVELOPMENTAL BIOLOGY -

Rooting the meristem

Gerd Jürgens

PLANT developmental biology was focused for a long time on groups of stem cells, the meristems of the shoot and root, that give rise to adult structures during postembryonic development. A large body of experimental evidence led to the traditional view that meristems are autonomous pattern-generating machines¹, producing the right kinds of organs and cell types at the right place. It seems ironical that the meristem with the most stereotyped arrangement of stem cells, the root meristem of the Arabidopsis seedling², has now failed the critical test. As reported by Scheres and colleagues on page 62 of this issue³, laser ablation of specific cells changes the fate of adjacent cells, indicating that the stem cells of the root meristem lack intrinsic patterngenerating information.

The root meristem is organized around a core of mitotically inactive cells termed the quiescent centre, which splits the stem cells into an upper and a lower tier of initial cells. While the lower tier adds new layers to the root cap, thereby shielding the root tip against mechanical destruction, the upper tier gives off daughter cells that extend the tissuespecific cell columns known as files which run the length of the growing $root^2$. In cross-sections of the root, the tissues are arranged in a radial pattern like the rings of a tree: the vascular tissue in the centre is surrounded by concentric layers of pericycle, endodermis, cortex and epidermis cells. Not only is the radial sequence of tissue layers fixed, but the number of cell files within each tissue is also invariant, or nearly so. For example, there are

always eight files each of cortex and endodermis cells derived from eight common stem cells which continually produce daughter cells that divide periclinally (radially) to give an outer cortex and an inner endodermis cell.

repeatedly in the same person at different

ages (before and after puberty, for example), there can be no definitive answer

as to whether these regions direct psycho-

logical sexual differentiation or are them-

mutually exclusive. It may be that some

are born with a predisposition to transsex-

uality and that social influences either

potentiate or attenuate this predisposi-

tion. Both predisposition and social influ-

ence would have to affect the brain

physically and the work of Zhou and col-

leagues suggests that the BSTc may be the

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Of course, these alternatives are not

selves directed by that process.

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In their elegant series of laser-ablation experiments, van den Berg et al.³ destroyed either stem cells or their daughter cells in order to determine the origin of cortex/endodermis cell fate. If an individual stem cell is ablated, the underlying pericycle stem cell divides abnormally and its outer daughter cell effectively takes over the function of a cortex/endodermis stem cell. If a single daughter cell is destroyed, the cortex/endodermis stem cell continues to function normally. But if three adjacent daughter cells are ablated, the central one of the three stem cells now produces daughter cells that fail to divide properly to give cortex and endodermis cells. If instead a radial set of three daughter cells, one each from epidermis, cortex/endodermis and pericycle, is eliminated, the cortex/endodermis stem cell continues to function normally. The authors conclude that the patterning information does not reside in the stem cells of the meristem themselves, but seems rather to be imparted by mature cells of the root.

In retrospect, the present results extend earlier observations made using different approaches. For example, basal amputation of older carrot somatic embryos resulted in proximo-distal regeneration of root and root meristem from the cut edge of the stump⁴, indicating that the remaining mature tissue has the information to reconstruct the missing body parts in an orderly way. Likewise, attempts to dissect seedling root development failed genetically but resulted in the isolation of mutants that altered the radial pattern of the body axis both in the embryo and post-embryonically^{5,6}. Interestingly, these mutants displayed the same pattern defects in lateral roots as well as in 'adventitious' roots regenerated from lumps of undifferentiated cells called callus, although both kinds of root have a non-embryonic origin.

The formation of lateral roots might shed some light on the role of the meristem in development. Initially, a small group of pericycle cells starts dividing, producing a lateral root primordium which subsequently forms at its tip a new meristem that is essentially organized like the primary root meristem of the seedling². If radial patterning occurs in the young lateral root primordium, the tissue pattern thus established might serve as a reference for the subsequent extension of the cell files by the root meristem.

Has the paradigm been turned around, making the former master of development its slave? The answer is, not really. The root meristem is not just a cluster of proliferating cells, supplying the plant body with raw material for continued growth. The root meristem has a specific organization, with its stem cells being arranged around a quiescent centre. This organization is restored following ablation of the quiescent centre³, or excision of the quiescent centre and the root cap⁷, suggesting that this central group of cells plays an as-yet undefined role in the functional organization of the root meristem⁸. One possible role of the quiescent centre could be to keep the physically adjacent stem cells dividing.

Unexpected results often raise more questions than can be answered. One of the most challenging tasks will be to determine the nature and origin of the root patterning signal(s). In view of a recent report on the cell wall and the plant extracellular matrix being involved in cell-fate determination in the brown alga *Fucus*⁹, we should be prepared to face more surprises in plant development.

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