

NECESSARY ASYMMETRIES IN BILATERALLY SYMMETRICAL BRAINS

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It is usually claimed that human brains, and all other brains having two apparently similar halves, have potential or actual bilateral symmetry^(1,2). Anatomical differences between the two sides of the brain in man are thus assumed to have functional significance because they constitute exceptions to a general rule of symmetry⁽³⁾. However, *any* brain that has neuronal cross-connections between the two sides must violate bilateral symmetry. Informally this can be seen by imagining the state of affairs at the mid-line of the corpus callosum of a mammalian brain that has absolute, neuron-for-neuron, bilateral symmetry. Nerve impulses attempting to cross the midline in this case would collide with their identical partners coming in the opposite direction. In order for this not to happen, there must be departures from bilateral symmetry in commissures such as the corpus callosum. Decussations like the optic chiasma must also be asymmetrical. Therefore, the duplicated crossing of both sensory and motor pathways, an apparently functionless design feature of vertebrate brains, may serve the purpose of increasing left-right differentiation.

More formally, consider a brain with identical halves on either side of the plane X at $x = 0$ on the left-right axis. In this three-dimensional object points can be identified by the axes z , x , y where z is longitudinal and y vertical.

(1) We begin by assuming that for every point $(z, -x, y)$ on the left, there exists a corresponding point $(z, +x, y)$ on the right. This is the assumption of bilateral or "mirror-plane" symmetry about the plane X⁽⁴⁾. (We should not expect symmetry about the other planes Z and Y). Can the bilateral symmetry about X be retained in the commissures and decussations which occur in profusion in all vertebrate brains⁽⁵⁾?

(2) *Commissures* are defined as continuous connections between a point P on the left $(z_h, -x_i, y_j)$ and its opposite number P' $(z_h, +x_i, y_j)$ on the right.

(3) *Decussations* are continuous connections between a point P $(z_h, -x_i, y_j)$ and a point Q' on the other side with different coordinates $(z_k, +x_i, y_m)$.

(4) *Unidirectionality*. To match real neurons commissures and decussations are assumed to be unidirectional. That is PP' is not the same as P'P and PQ' would not be the same as Q'P.

(5) *Occupation of space*. Again to correspond to real neurons, we assume that any individual connection across the brain occupies space, and that two connections cannot therefore share the same space at any point.

(6) *Asymmetry in commissures*. Can there be a symmetrical interconnection between the identical but opposite points P and P'?

In order for P and P' to be symmetrically connected there must be both a connection PP' and a connection P'P (see (4) above) and PP' and P'P cannot follow the same path (see (5) above). Consider the intersections of PP' and P'P with the plane X. Since the two connections cannot occupy the same point on X, they must occupy different points on X. That is, when $x = 0$, the y and/or z coordinates of PP' and P'P must differ. Thus as PP' approaches X, a point on PP' must differ from any corresponding point on P'P in its y and/or z coordinate, and therefore at such a point PP' and P'P do not have mirror-plane symmetry about X (see (1) above).

(7) *Asymmetry in decussations.* In practice commissures might not be expected to connect mirror points, but merely mirror regions of points⁽⁶⁾. Geometrically this arrangement may be treated as a decussation, since a point on one side is connected to a point on the other side which is not identically opposite. For either this case or for more obvious decussations, the question is if the connection PQ' between $P(z_h, -x_i, y_j)$ and $Q'(z_k, +x_i, y_m)$ can have mirror-plane symmetry with the connection P'Q between $P'(z_h, +x_i, y_j)$ and $Q(z_k, -x_i, y_m)$.

Both PQ' and P'Q intersect the plane X, as x changes sign. Since they cannot intersect at the same point (see (5) above) they must intersect X at different points and hence they are bilaterally asymmetrical about X in the same way as commissures.

Countless children must have asked why Alice did not bump into another little girl when she attempted to climb through the Looking Glass. Lewis Carroll⁽⁷⁾ made the other side of the glass a different world: if he had not, Alice would have had to adopt some sort of asymmetrical dodging manoeuvre with her alter-ego. Similarly, if brains are to have any neurons which cross the midline, they must either have halves which are different from one another, or use asymmetrical interdigitation of the cross-connecting neurons. The geometric necessity of this is rarely, if ever, acknowledged^(1,2,8). Grounds for continuing to ignore these inherent asymmetries would be that they are trivial in practice since their magnitude could be of the order of the width of a neuron, or that the asymmetries may be confined to the cross-connections of a brain where they would be expected to have little functional significance. Even the functional significance of the quite large anatomical asymmetries that are known to exist in the human cerebral hemispheres is uncertain^(3,9). Although larger areas in the left temporal lobe of human brains are thought to reflect left-hemisphere dominance of speech, the physical superiorities of the right frontal lobe (including "Broca's region"⁽¹⁰⁾) and the left occipital lobe over their counterparts lack equivalent interpretations^(3,9). The explanation for the noticeable asymmetries in the habenular nuclei of lower vertebrates likewise remains a mystery⁽¹⁾.

However, a general rule of asymmetry in vertebrate brains may be applied if asymmetries induced in or by cross-connections are taken into account.

The ubiquity of commissures and decussations in vertebrate brains is explicable partly in terms of "crossed lateral control": sensory information from the left tends to be projected to the right side of the brain, which in turn controls the left side of the body, while right-sided information is dealt with by the left half of the brain⁽¹⁾. It has been shown above that all the cross-connections which this involves are necessarily asymmetrical, and the actual magnitude of such irregularities is not always negligible. For instance, the crossing of the optic nerves in teleost fish is usually accomplished by one optic nerve going completely below the other^(12,13). In many lower vertebrates, the optic nerve from one eye divides into two bundles, which interlace with three bundles from the other⁽¹²⁾. A similar plating of bundles of fibres is visible in the decussation of the pyramidal motor tracts in the human brain-stem. There is usually what Kertesz and Geschwind call a "right-of-way" for bundles from the left hemisphere to cross over first, although there are enormous individual variations, not having any clear relation to handedness⁽¹⁴⁾.

The reason why vertebrate brains should employ the strategy of crossed-lateral control, requiring the decussation of both sensory and motor pathways, has always been a puzzle^(1,15), and the problematical nature of midline crossings, emphasised here, makes the arrangement seem even more perverse. That is, unless the asymmetry introduced by decussations is an advantage: one reason for crossed-lateral control may be that it increases left-right differentiation in otherwise bilaterally symmetrical brains. Why the asymmetries imposed by decussation should be adaptive is, of course, another question.

It is hard to see how mirror plane asymmetries at the midline of cross-connections might affect the visible anatomy of the cerebral hemisphere. However, a significant correlation has been found⁽¹⁶⁾, in a series of 103 human brains, between the sectional area of the anterior commissure and the magnitude of the difference in size between the planum temporale of the two temporal lobes. Since in primates the anterior commissure cross-projects substantially to some regions of the cortex of the temporal lobes⁽⁸⁾, such a correlation might be expected if commissural and cortical asymmetries are interdependent in some way. In the human corpus callosum, as many as 100 million neurons may cross from one hemisphere to the other, interdigitating with another 100 million coming in the opposite direction⁽⁸⁾. Although there are no grounds for predicting any unavoidable consequences, it would hardly be surprising if bilateral asymmetries emerged in the areas connected by the corpus callosum, in particular the surfaces of the frontal, parietal and occipital lobes. Apart from asymmetries in the details of cortical convolutions, computerized tomography of human brains shows that there is commonly what Lemay calls “anticlockwise torque”⁽¹⁷⁾. The right frontal lobe tends to be wider than the left, and may extend farther forward anteriorly, while the left occipital lobe is often wider than the right one, and usually protrudes posteriorly beyond the right one. Could it be that during embryological growth, callosal axons crossing from left to right tend to deflect anteriorly, whereas those crossing from right to left more often deflect posteriorly? If cortical growth is stimulated at the terminations of callosal axons, the cumulative effect of this particular form of commissural asymmetry might produce the observed anticlockwise torque of the human hemispheres.

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