EXTRACT FROM

THE NEUROPHYSIOLOGY OF POSTURAL MECHANISMS

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Chapter 10 — Reflexes of Balance (pages 226-228)

The information from the labyrinth is used by the central nervous system, in conjunction with information derived from other receptors, in the formulation of an important class of reflex responses: the reflexes of balance. Under this heading we distinguish acceleratory reflexes from the semi-circular canals, and positional reflexes initiated from a variety of other receptors, including the otolith organs in the labyrinth. The acceleratory reflexes are responses to angular accelerations of the skull. Linear accelerations are associated with changes in the magnitude and direction of the resultant of the supporting contact forces. There is no way in which the various components contributing to this resultant can be distinguished by the animal. Accordingly the responses to imposed linear accelerations are included under the heading of positional reflexes.

The reflexes of balance serve to stabilize the attitudes of the head and trunk, to stabilize the direction of gaze of the eyeballs when the head moves, and to adjust the attitudes of the limbs and neck to compensate for asymmetries in the disposition of available supports. If the combination of stabilization and compensation fails to preserve balance, another set of responses, the 'rescue reactions' (p. 273) are initiated at the point of overbalancing. The 'righting reflexes' (p. 282) come into play after a displacement, to restore the head and body toward a standard 'normal' attitude.

It must be understood that there is a conflict between the requirement for stability, in which a specific attitude is maintained in the face of external perturbations, and the requirement for mobility, to permit the animal to execute the various movements that constitute its natural behaviour, be it voluntary or innate. If the stabilizing mechanisms were absolute, no change in attitude would be possible; any attempt to move would be countered by reflex adjustments tending to restore the normal attitude. On the other hand, if the stabilizing mechanisms need to be disabled to permit voluntary movements, all the benefits of stabilization are lost, and the animal is in danger of losing its balance. In this chapter we examine some of the ways in which animals escape from this dilemma and preserve their freedom of movement while retaining effective automatic stabilization for the maintenance of balance.

As an introduction to the general plan of the reflexes of balance, let us consider the effect of angular accelerations on the position of the eyes in the head. It is convenient to start here because we have only one class of receptor concerned with angular acceleration, namely the receptors in the semi-circular canals. However, we must not lose sight of the fact that angular acceleration implies a change in orientation, so that there may be concomitant stimulation of receptors in the otolith organs. Furthermore, a movement of the skull may involve a change in the angles of the intervertebral joints in the neck, and the receptors in these joints also play an important part in the reflexes of balance.

Leaving these other receptors aside for the moment, let us concentrate our attention on the canals. There are three canals on each side of the head, each with its own ampullary sense-organ. It is convenient to think of the canals as lying in three mutually perpendicular planes, although this is not strictly true. In some animals the canals follow a very sinuous course, so that it is difficult to decide what should be taken as 'the plane of the canal'. Sometimes the angles between the planes differ considerably from a right angle. In many cases the planes of the canals are neither vertical nor horizontal. Nevertheless, no serious confusions arise from giving to the three canals on each side the following three names: 'anterior vertical', 'posterior vertical' and 'horizontal'. In any particular skull it is easy to decide which canal is intended by each name.

It is much more difficult to decide the positions of the planes of the canals in relation to externally defined vertical and horizontal directions such as those given by the Earth's horizon. We cannot examine the canals directly in the living animal, even with x-rays, because of the confusing shadows of other bony irregularities in the same region. We must, therefore, first define the orientation of the skull, and then localize the canals in the skull by dissection.

The orientation of a body is defined by the directions in space of any two non-parallel lines through fixed points on the body. Now, because the plane of symmetry of the head is vertical when the head is in the 'normal' position, we can take as one of our reference lines the line running through the centre of the external auditory meatus on the two sides. Clearly this line must be horizontal and there is no difficulty here. The problem lies in what to take as the second reference line.

In many ungulates the profile of the frontal and nasal bones gives an obvious straight line, and in a lateral view of a domestic cow, for example, it is easy to measure the inclination of this line to the vertical. Animals of different species show characteristic differences in the attitudes of their heads as measured in this way. For example, the bison normally carries its head with the front profile nearly vertical, whereas in the camel the corresponding line is almost horizontal.

In man, and indeed in most animals, there are no obvious straight lines in the profile, or on the skull, to serve as guides. Many points of reference have been proposed. The lower margin of the orbit is often used, together with the upper margin of the external auditory meatus, to provide a standard plane for purposes of anthropometry[1]. A plane so defined does not necessarily correspond with the horizontal when the head is in the characteristic position for the animal. This point must be borne in mind when considering reports of the orientation of the canals in the skull. If the standard measurement plane is taken as horizontal, the plane of the 'horizontal' canal will appear inclined, at an angle which is different for different species. This is the situation reported in many anatomical texts.

However, if account is taken of the normal carriage of the head and of the consequent inclination of the reference plane, it has been found that, for some 30 species of mammals and for some 20 species of birds, each animal characteristically carries the plane of its 'horizontal' canal very nearly parallel to the horizon[2].

We may apply the argument in reverse to decide what should count as the 'normal' position of the head in man. When the horizontal semi-circular canal is parallel to the horizon, the head is in the position characteristic for a boxer on the alert to defend his equilibrium. It corresponds to the attitude commonly used for reading, for examining something held in the hand, or for walking over rough ground. In contrast, bringing the anthropometric reference plane into the horizontal position gives the head the unnaturally elevated attitude of a military parade.

The planes of the 'vertical' canals are arranged diagonally across the skull, so that the anterior vertical canal of one side lies in a plane parallel to that of the posterior vertical canal of the opposite side (see Figure 10.1). The utriculus lies near the point of intersection of the planes of the canals. It is usual for two of the canals to share a common opening into the utriculus. These are not always the same two, as may be seen in Figures 9.3 and 9.2. Further examples may be found in the important monographs on labyrinth structure by Retzius and by Gray. The ampullae of the vertical canals lie near the lower and outer parts of the canal, while the ampulla of the horizontal canal lies near its anterior connection with the utriculus.

As has been explained in the previous chapter, the neuromasts of the cristae of the canals give rise to a continuous stream of impulses in their afferent nerves even when the skull is at rest. Angular accelerations about an axis through the centre of the circle formed by the canal produce increases or decreases in the frequency of the impulses according to the direction of deflection of the cupula. In the vertical canals the increase in discharge occurs when the angular acceleration is in the 'ampulla-leading' direction, whereas in the horizontal canal the increase in discharge occurs during angular acceleration in the 'ampulla-trailing' direction. 'Ampulla-leading', for the right anterior vertical canal, means tipping the anterior right-hand corner of the skull downwards over a diagonally placed horizontal axis.

Figure 10.1 (above) Schematic plan view of the head of a mammal to show the disposition of the planes of the vertical semi-circular canals.

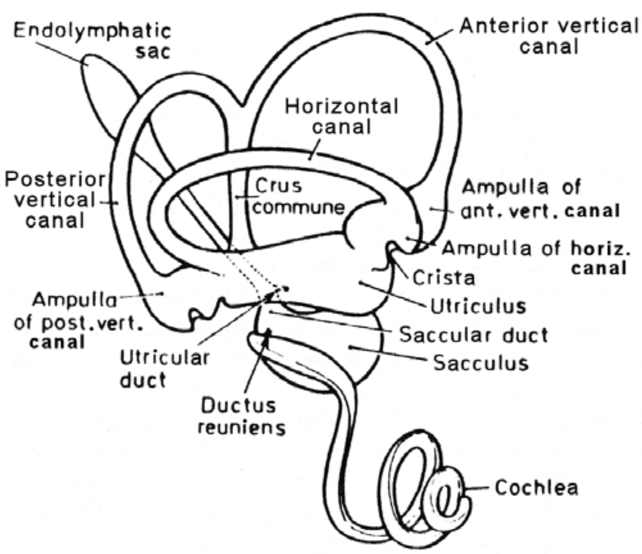

Figure 9.2 (left) Sketch of the labyrinth of the right ear of a guinea pig seen from a little below and behind the interaural line. The endolymph cavity of the cochlea communicates with the cavity of the sacculus by the ductus reuniens. Sacculus and endolymphatic sac in turn communicate with the utriculus, which also receives all the openings of the semicircular canals. The endolymph cavities of the whole labyrinth thus form a continuous closed system of bags and tubes.

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[1] *Note by DG*: This is the so-called 'Frankfort plane'. The '*external auditory meatus*' is the outer ear hole.

[2] *Note by DG*: This is from research by Prof. G. R. de Beer summarized in his paper "*How Animals Hold Their Heads*" (*Proceedings of the Linnean Society of London*, Volume 159, Issue 2, pages 125–139, December 1947)