HOW ANIMALS HOLD THEIR HEADS

Presidential Address by **Professor G. R. De Beer**, F.R.S., P.L.S.
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(With 19 text-figures.)

The subject which I have chosen for the customary Address this year lays no claim to authoritativeness ; it is not a wide synthesis of the state of knowledge reached in any particular field ; nor does it pretend to any particular intrinsic importance. I have preferred to take my audience into my confidence and to go, with them, through the results of a few observations and experiments which I have made and conducted myself during the past few months. The subject is a very simple one : how animals hold their heads ; in fact so simple that few have considered it worth their while to pay attention to it. I have selected it as my subject for today, not only because it has interested me but also for another reason, closely connected with the constitution and membership of this Society. The Linnean Society occupies a position, perhaps unique, in that it combines the interest and points of view of the systematic and the academic biologist, the professional, the naturalist and the amateur. Collaboration between all these types of biologists is of the highest importance for the successful prosecution of our science, and in what I have to say I hope that I shall succeed in making it clear that the amateur will have as much, if not more, to contribute than the professional.

My own interest in the problem of the posture of the head in animals arose from some work which I had previously done in connexion with the development of the skull.

It is well known that on each side of the head vertebrate animals have three semicircular canals, orientated at right angles to one another, in the three planes of space, movements in any or all of which are appreciated by the appropriate canals.

The planes of the canals are easily discernible in the skulls, both of embryos and of adults, since they are enclosed within the cartilage or bone of the auditory capsule. I am going to concern myself only with the pair of semicircular canals known as the lateral or horizontal pair, and the first thing which excited my curiosity was the fact that, during development, the plane of these-canals underwent a change relatively to the plane of the base of the skull. This was interesting in itself, showing that the plane of the canal in the adult animal is only reached as a result of certain modifications during development, and must presumably have a meaning. This became all the more probable when I realized that while the rotation of the plane of the lateral semicircular canal relatively to the plane of the base of the skull took place in one direction' (clockwise when seen from the left side) in most mammals, in others, including man, it took place in precisely the opposite direction (counter-clockwise when seen from the left side).

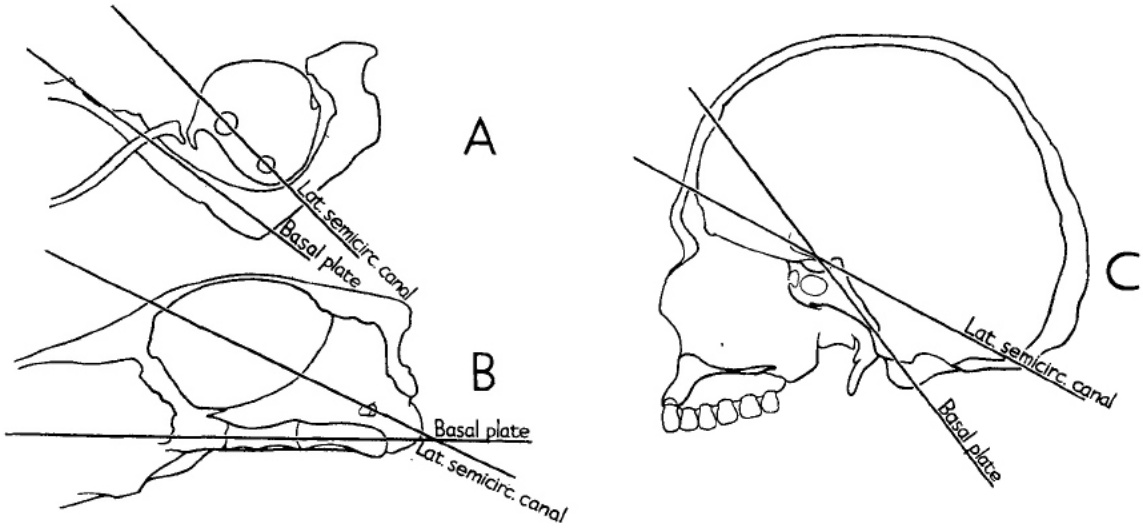

Fig. 1.—Diagram showing the relations between the plane of the lateral semicircular canal and the plane of the floor of the skull (basal plate) in
A. The embryonic condition (chondrocranium of rabbit), with the planes almost parallel ;
B. Adult horse's skull, with the plane of the lateral semicircular canal rotated clockwise relatively to the plane of the basal plate when seen from the left side ;
C. Adult man's skull, with the plane of the lateral semicircular canal rotated counterclockwise relatively to that of the basal plate when seen from the left side.

There must be clearly some good reason why, during development, animals. go to so much trouble to rotate the planes of their lateral semicircular canals, and the obvious hypothesis to invoke is one which has been invoked by Girard in France and by Lebedkin in Russia, namely, to suppose that the rotation takes place in such a way that the result is to leave the lateral semicircular canals in the horizontal plane when the animal is adult.

This apparently simple hypothesis in fact, however, presupposes a very important corollary, which is that animals have a characteristic and constant position of holding their heads. Previous workers, including those whom I have named, did not hesitate to start from the assumption that animals do in fact hold their heads in such a position that their lateral semicircular

canals are horizontal. But this was taking for granted precisely what I wanted to prove. And, as I shall be able to show, there was a considerable surprise in store.

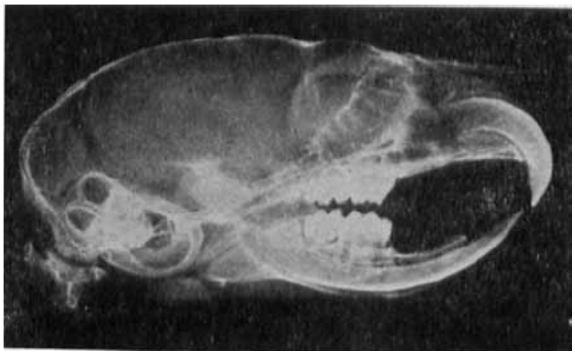

Fig. 2.—Radiogram of skull of adult mouse, showing the planes of the lateral semicircular canal and of the basal plate. (courtesy Prof. Amoroso, Royal Veterinary College.)

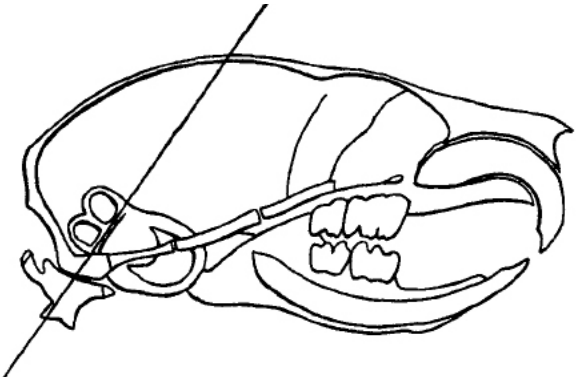

Fig. 3.—Outline projection of fig. 2. A straight line is drawn through the plane of the lateral semicircular canal.

It has been known ever since the magnificent researches of Magnus that the nervous and muscular mechanisms of the bodies of animals are so arranged that when the position of the body of an animal is artificially upset, the muscles are automatically stimulated to contract and extend in such a way as to restore the head to its original position, and it is also known that the ear is responsible for starting the chain of stimuli which result in this rectifying mechanism. It had, however, not been shown whether the position to which the head is, restored in this way is the one in which the lateral semicircular canals are horizontal. It was therefore necessary for me to determine what is the plane of the lateral semicircular canal in an animal, whether the animal has a constant characteristic position in which it holds its head, and what, at that position, is the plane of its lateral semicircular canal relatively to the horizontal.

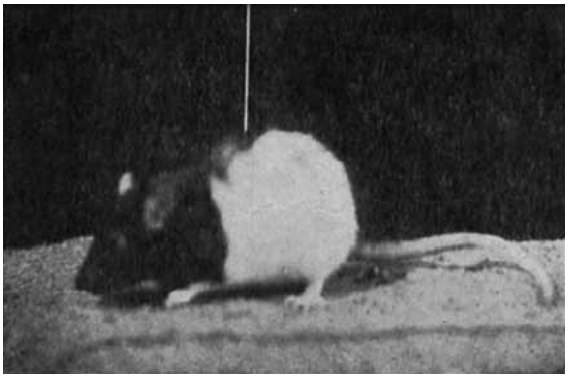

Fig. 4.—Photograph of live mouse in state of alertness against a plumb-line.

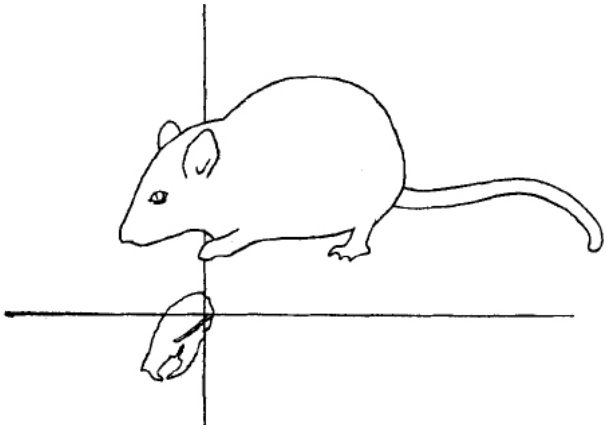

Fig. 5.—Assemblage of live mouse on vertical axis of plumb-line and mouse skull with plane of lateral semicircular canal drawn at right-angles to plumb-line. In the position of alertness the mouse therefore holds its head in a position in which the plane of the lateral semicircular canal is approximately horizontal.

A further question which at once arises is the state of the animal when it adopts this position. I have assumed that it must be a state of alertness, but it might be alertness to smell, to sound, or to sight. For reasons which I shall give later, I think that it is alertness to sight that is concerned here. Meanwhile this digression will serve to introduce a fact of some significance ; viz., that the problem introduces us to a great many fields ; in this case to those of sense-physiology and to the bionomics and behaviour of the animals.

The ideal procedure would, of course, be to take an X-ray photograph of the living animal, in a state of alertness, against a plumb-line, so as to gather all the required information on one negative. This is, however, not practicable, and it is necessary to proceed by instalments. First of all, the plane of the lateral semicircular canal can be determined in the skull by X-rays ; next, the normal position of the head of the alert animal can be determined by ordinary photography against a plumb-line ; and finally, the two results can be combined on one diagram in order to see what angle the plane of the lateral semicircular canals makes with the plumb-line.

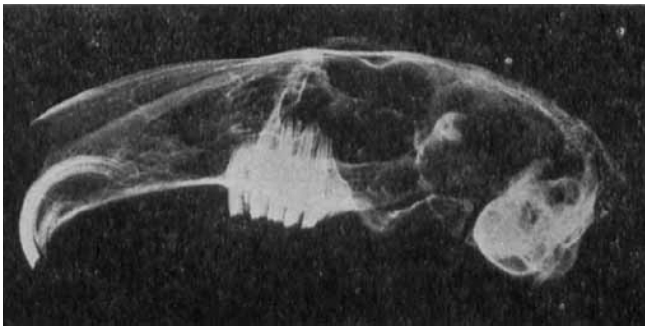

Fig. 6.—Radiogram of skull of adult rabbit, showing the plane of the lateral semicircular canal.

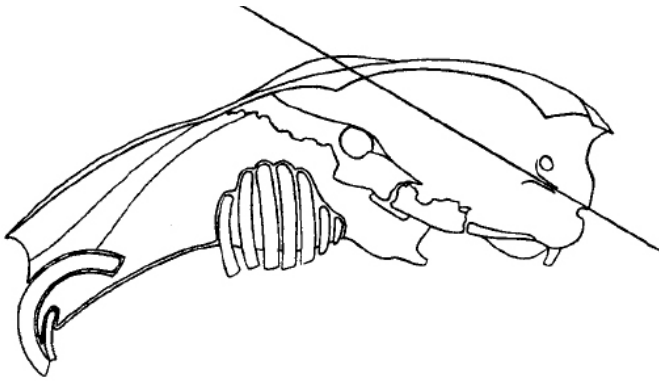

Fig. 7.—Outline projection of fig. 6. A straight line is drawn through the plane of the lateral semicircular canal.

Fig. 2 is a radiogram of a mouse skull in which the plane of the lateral semicircular canal is easily discernible, and in fig. 3 it has been projected on to an outline drawing. Fig. 4 is a photograph of a live mouse in what I believe to be its normal alert position, taken against a plumb-line. Fig. 5 is an assemblage of the information provided by the radiograms of the skull and by the live mouse, made in such a way that the plane of the lateral semicircular canal is orientated at right-angles to the axis of the plumb-line. It will be seen that the outline of the skull fits well into the outline of the head. of the live animal, and I therefore conclude that the lateral semicircular canal is approximately horizontal in the live animal. I say approximately, for,. with the simple methods used, a perfect degree of accuracy cannot be expected. In addition, it has to be assumed that the structure of the live mouse was similar to that of the skull, which I have no serious reason to doubt.

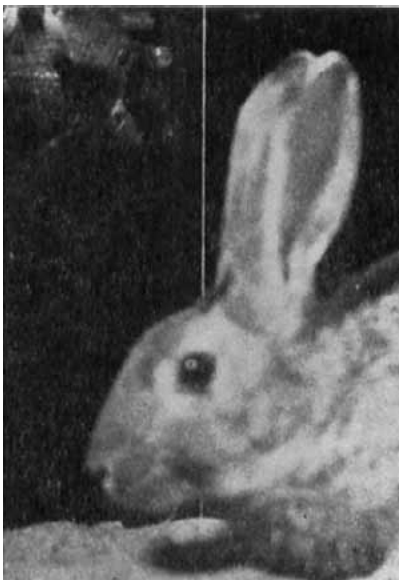

Fig. 8.—Photograph of live rabbit in state of alertness against a plumb-line.

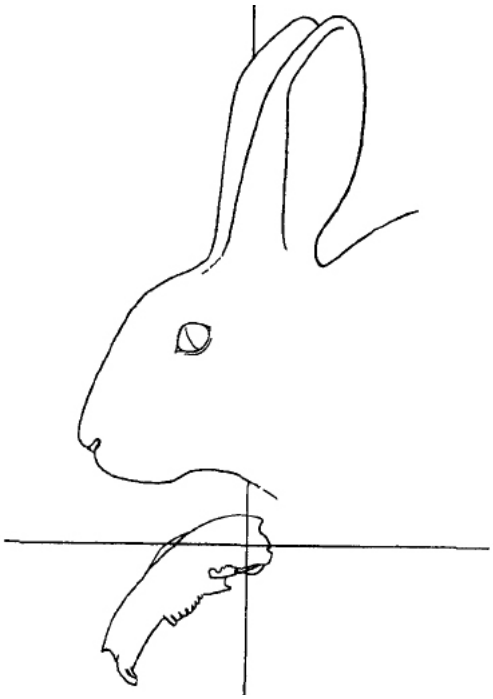

Fig. 9.—Assemblage of live rabbit on vertical axis of plumb-line and rabbit skull with plane of lateral semicircular canal drawn at right-angles to plumb-line. In the position of alertness the rabbit therefore holds its head in a position in which the plane of the lateral semicircular canal is approximately horizontal.

The next set of figures repeats the same technique on the rabbit. Fig. 6 is the radiogram ; fig. 7 is the projection of the plane of the lateral semicircular canal on to the line drawing ; fig. 8 the live rabbit, and fig. 9 the assemblage, which again shows that the plane of the lateral semicircular canal is approximately horizontal in the live rabbit.

In larger animals, in which the bone of the skull is thicker and more opaque, it is not practicable to make out the plane of the lateral semicircular canal in the skull by means of X-rays. I have therefore had to have recourse to. the method of dissection, which is not only more laborious, since the canal has to be exposed by a dental drill and a coloured bristle passed through the canal, but also more liable to error. However, such as it is, fig. 10 shows the outline of the skull of the horse as seen in a view from the medial side of the left half of the skull, with the plane of the lateral semicircular canal projected on to it. Fig. 11 is the live horse with the corner of a wall conveniently serving as a plumb-line ; and fig. 12 is the assemblage, again showing that the position of the lateral semicircular canal is approximately horizontal.

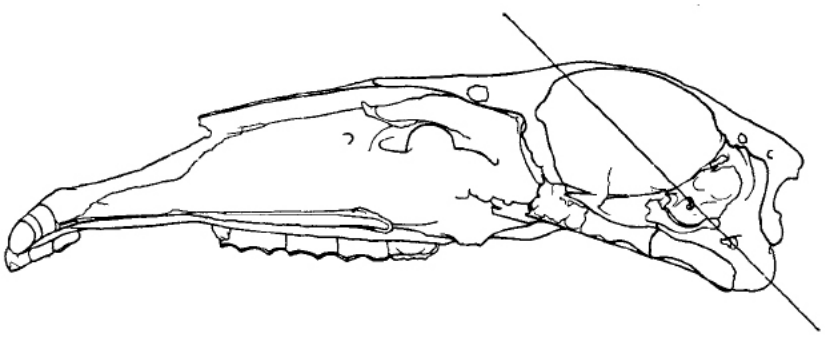

Fig. 10.—Outline drawing from medial side of left half of skull of adult horse. The plane of the lateral semicircular canal has been made out by dissection and is projected on to the drawing.

My next example is the dog. Fig. 13 shows a view from the medial side of the left half of a skull with the plane of the lateral semicircular canal, as determined by dissection, projected on to it. Fig. 14 is the live dog and fig. 15 the assemblage. The fit here is not quite so good, and I have the impression that the dog was looking slightly upwards when the photograph was taken, which means that in that position its lateral semicircular canals were sloping slightly backwards and downwards. This introduces yet another feature into the problem. For while in the other animals that I have described there does appear to be an approximation to the horizontal position for the plane of the lateral semicircular canals at positions of the head which I think can be reasonably described as those of normal alertness, the animals are of course capable of putting their heads into other positions. We shall have to see later whether this is less advantageous for them, but meanwhile we must note that in an intelligent and inquisitive animal like the dog, the plane in which the lateral semicircular canals is held is likely to be varied, particularly when it is sniffing and scenting.

Fig. 11.—Photograph of live horse in state of alertness against a vertical corner of a wall.

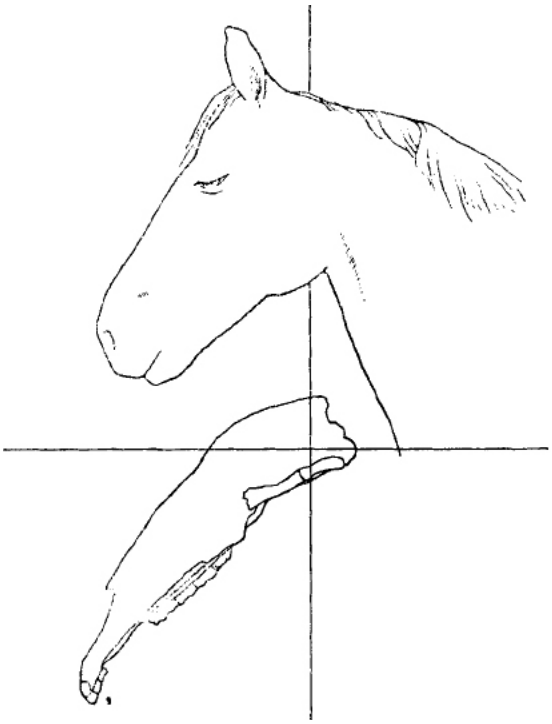

Fig. 12.—Assemblage of live horse on vertical axis and horse's skull with plane of lateral semicircular canal drawn at right-angles to the vertical axis. In the position of alertness, therefore, the horse holds its head in a position in which the plane of the lateral semicircular canal is approximately horizontal.

When we come to man, the conditions are rather peculiar. The human skull does not permit of determination of the plane of the lateral semicircular canal by X-rays ; nor does the human head lend itself easily to the superposition of an outline projection of the skull on a profile of the living subject, owing to the lack of a long axis. The method which I have adopted is therefore indirect. First of all the plane of the lateral semicircular canal in the dry skull is determined by dissection, and projected on to a radiogram of the skull. Next, the so-called Frankfort plane is determined, the plane which passes through the lower border of the eye-socket and the upper border of the external auditory meatus. This is also projected on to the radiogram of the skull, and the angle is measured between these two planes. The advantage of this is that the Frankfort plane is easily discernible in radiograms of the living subject.

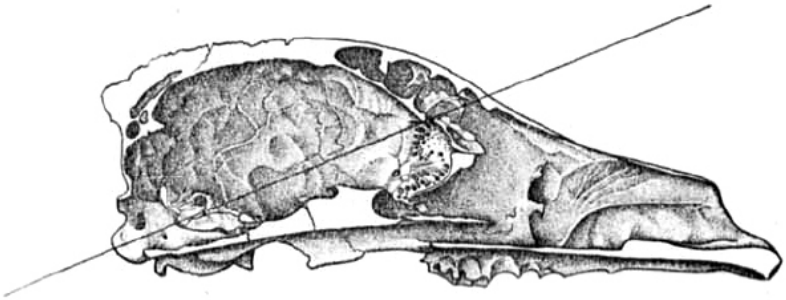

Fig. 13.—Outline drawing from the medial side of the left half of the skull of an adult dog (greyhound). The plane of the lateral semicircular canal has been made out by dissection and is projected on to the drawing.

Fig. 16 shows the plane of the lateral semicircular canal and the Frankfort plane as projected on to the radiogram of a dry skull. These planes make an angle of about 30°, and they are shown also in fig. 17, which is a view from the medial side of the left half of a skull. I am aware that there is variation in the angle which these planes make, as shown by the researches of Schönemann, albeit, by a very indirect method. After sawing out the bony auditory capsule by a cut parallel with the Frankfort plane, filling it with Wood's metal and then dissolving away the bone, he found as much as 30° of variation between the plane of the lateral semicircular canal and the cut surface. By another method, using the position of the supra-orbital ridge as a standard, Girard found that the angle which the plane of the lateral semicircular canal made relatively to this ridge varied by 25°. On the whole, however, the general tendency of otologists, from Crum Brown to Watkyns-Thomas and Lowndes Yates, is to agree that the plane of the lateral semicircular canal in man usually makes an angle of 30° sloping downwards and backwards from what they call the horizontal.

Fig. 14. —Photograph of live dog in state of alertness against a vertical corner of a wall.

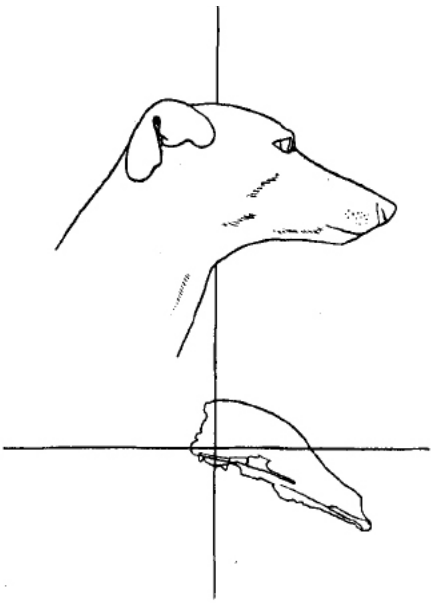

Fig. 15.—Assemblage of live dog on vertical axis and dog's skull with plane of lateral semicircular canal drawn at right-angles to the vertical axis. In the position in which the dog is holding its head, the plane of the lateral semicircular canal deviates slightly from the horizontal.

Now the Frankfort plane was adopted by anthropologists as the best practical approximation to the horizontal, but I cannot trace any actual experiments designed to show what in fact is the position of the Frankfort plane at normal positions ' of the head in man, nor what such a position is. I have accordingly conducted an experiment on ten students of my department. When dealing with the human subject it is very necessary to guard against any possibility of subjective influences interfering with the conditions of the experiment. If I had told them that I wanted to study the position in which they hold their heads, they would inevitably have posed. Some would have consciously tried to stand in what they considered to be the normal position ; others, and especially those who have had military service, would have stood at the position of attention. I therefore adopted the expedient of concealing from them what my object really was, and I asked them to stand before the X-ray camera facing at right-angles to the axis of the camera, and to turn their heads towards the camera and back again. They were snapped as soon as they had turned their heads to their front, and they were then asked to say what mark their eyes were resting on upon a scale placed in front of them. By this means I obtained values not only for the angle between the Frankfort plane and the vertical plumb-line, but also for their angle of sight, since the height of the pupils of their eyes was also known.

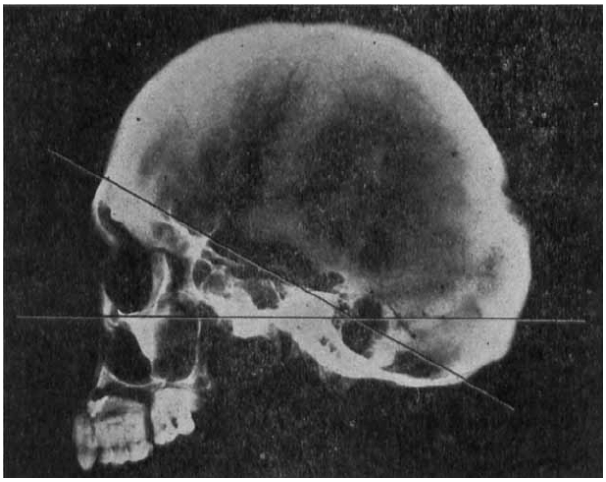

Fig. 16.—Radiogram of skull of adult man, showing the relation between the planes of the Frankfort line (passing through the lowermost border of the eye-socket and the uppermost border of the external auditory meatus ; both of which have been pointed on the skull by a piece of metal) and of the lateral semicircular canal which has been made out by dissection and projected on to the radiogram. These planes make an angle of approximately 30°.

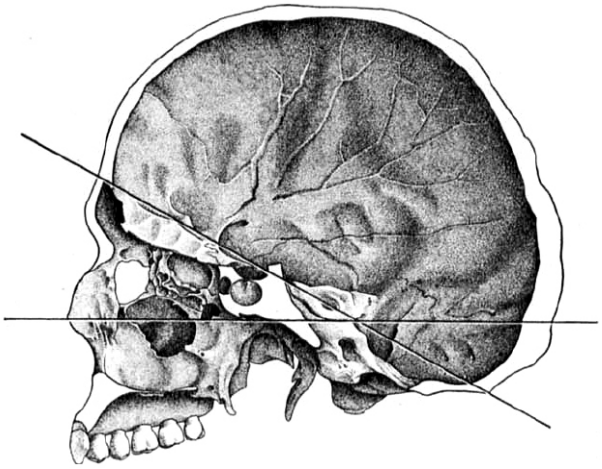

Fig. 17.—Drawing from the medial side of the left half of the skull of adult man shown in fig. 16, with the planes of the Frankfort line and of the lateral semicircular canal projected on to it.

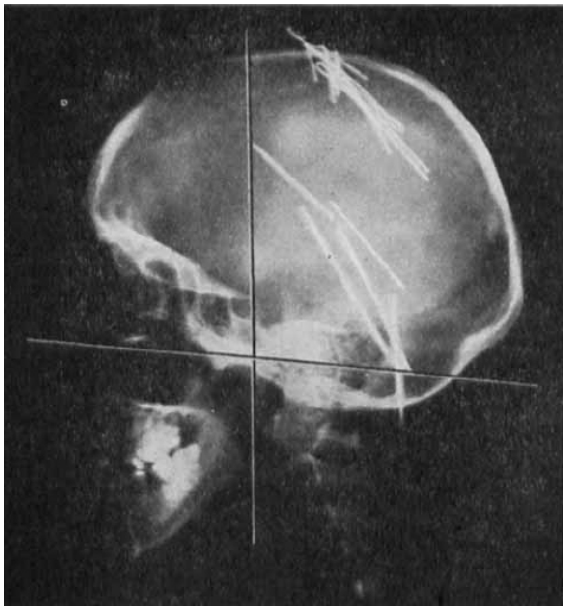

Fig. 18.—Radiogram of living human subject in 'normal' position against vertical axis. The plane of the Frankfort line slopes 7º backwards and downwards from the horizontal ; the plane of the lateral semicircular canal presumably slopes approximately 37° downwards and backwards.

The following are the results obtained :—

Serial number	Angle of Sight	Angle between vertical and Frankfort plane	Angle between horizontal and Frankfort plane *
1 —	7º	96°	-6°
2 —	9° 30'	95°	-5°
3 —	7º 30'	96°	-6°
4 —	7º 30'	95°	-5°
5 —	7º	84°	+6°
6 —	7º	95°	-5°
7 —	7º 30'	88°	+2°
8 —	7º 30'	97°	-7°
9 —	8º	87°	+3°
10 —	9º	87°	+3°

** The rightmost column is not in the original paper but is added to further clarify the orientation of the head relative to horizontal*

Fig. 18 shows the subject with the maximum backward slope of the Frankfort plane, and fig. 19 the subject with the maximum forward slope of that plane.

It will be noticed that the Frankfort plane does not deviate by more than 7° below the horizontal or 6° above the horizontal. As a standard, therefore, the Frankfort plane is a good rough approximation to the horizontal position.

It is also to be noticed that in spite of the variation of the Frankfort plane to the horizontal, all the subjects showed a remarkable constancy in their angles of sight, not varying by more than 3°. It was presumed by Broca many years ago that the normal position of the head of an organism was that in which the eyes were directed on to the horizon. I am also informed by my friend, Dr. Nigel Cridland, that it is generally accepted by ophthalmologists that the primary position of gaze is horizontal. The number of subjects on which I have worked is of course too small to base any far-reaching conclusions. on the results, but it may be of interest to ophthalmologists to investigate it further.

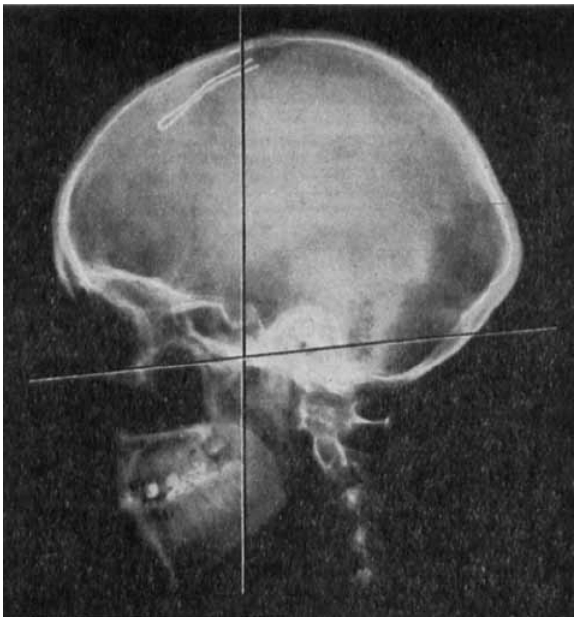

Fig. 19.—Radiogram of living human subject in 'normal' position against vertical axis The plane of the Frankfort line slopes 6° forwards and downwards from the horizontal ; the plane of the lateral semi-circular canal presumably slopes approximately 24° backwards and downwards from the horizontal.

Meanwhile, to return to the plane of the lateral semicircular canals in many it will be seen that if that plane is taken as differing from the Frankfort plane by 30°, then its deviation from the horizontal will vary between 24° and 37°. In any case, and this is the important thing, if we leave out of account the variations between the plane of the lateral semicircular canals and the Frankfort plane (which cannot be determined in the living subject), at positions of the head which appear to be normal in man, the plane of the lateral semicircular canals differ considerably from the horizontal, sloping backwards and downwards by something like 30°. It is therefore an error of fact for Lebedkin to claim, as he did, that this plane is horizontal.

If man wishes to place his lateral semicircular canals in the horizontal position, he must bend his head forwards and downwards. From the projection of the plane of the lateral semicircular canal on to the outline of the dry skull, Girard described the condition in man by saying that the plane of these canals would be horizontal if a man looked on to the ground at a point one or two metres in front of him.

The position of the plane of the lateral semicircular canals in man may perhaps be of special interest to anthropology in connexion with the descent of man from his pre-human ancestors, for in modern anthropoids the position of the foramen magnum is further back, and they stick their heads out forwards and downwards instead of balancing them on the top of a vertical neck. It is therefore possible that modern man may have retained something of the characteristics of his ancestors in the plane of the lateral semicircular canal.

The problem now arises, if mammals generally hold their heads in such a position that their lateral semicircular canals are horizontal, what advantage does it confer on them, and why does man differ and forego such an advantage? The answer to this problem entails a digression into some very important questions of sense-physiology and behaviourism. It might be thought, since the three semicircular canals on each side are at right-angles to one another, that it was immaterial what their exact orientation was, as movement in any direction in space would be resolved along one or more of their axes. It has, however, been shown, largely by the work of Dr. Löwenstein, that the sense-organs of a semicircular canal are in a condition of maximum reactivity when the motion to which they are subjected and respond is in the same plane as that of the canal. When an animal in a state of visual alertness turns its head and looks around, which is a reaction of the utmost importance to many animals in the detection of enemies, its sense-organs of balance will therefore function at their maximum efficiency if the lateral semicircular canals lie in the plane of such head-rotation, which will of course tend to be the horizontal.

There is an additional possible reason why this arrangement is beneficial. From the work of McNally and Tait on the functions of the sense-organs of the semicircular canals in the frog, the interesting result emerged that whereas the vertical canals produced a unilateral effect on the tonus of the muscles of the body, the lateral canals produced a symmetrical effect on the muscles of both sides of the body. The condition in which the lateral semicircular canals are horizontal is therefore

the one in which the vertical canals will experience the least stimulation when the head is rotated. It would therefore be expected that there would be the minimum unilateral interference with the tonus of the body-muscles, and that, after a vigorous rotation of the head, the animal would not lurch sideways and fall over, as it might if its muscles were subjected to unilateral stimulation.

It would be expected therefore that defenceless animals which depend greatly for their safety on rapid scanning of the horizon, would show the closest approximation of the plane of the lateral semicircular canal to the horizontal. When it comes to the question why this state of affairs does not apply to man, the answer is no doubt connected with the greater variability of the plane of the lateral semicircular canal found in man. The mechanism is no longer of importance, and man relies more on visual stimuli to control his posture. It may also be less important for him to scan the horizon by rapid rotation of the head.

In other animals, however, and there is no reason to think that birds and reptiles will be found not to agree with mammals, it does appear, from those which have been critically examined, that the plane of the lateral semicircular canal may reveal the position in which the animal holds its head. If this could only be established for a sufficiently large number of animals, there would be an interesting consequence for palaeontology. It might then be possible to determine how fossil animals held their heads, and in many cases, like those of the Dinosaurs and Titanotheres, this would be of considerable interest.

Now this is a field to which the amateur and the naturalist can contribute as much if not more than the professional academic biologist. What is required is the widest possible range of observations. The plane of the lateral semicircular canal can easily be found by a, simple dissection of the skull. In bats no dissection is needed, for the canals are each enclosed in their own bony tube instead of being embedded in a compact bony capsule. In birds, the canals can be found with the greatest of ease, for the auditory capsule is composed of spongy bone which can be chipped away revealing the canals of harder material. The observation of the living animal requires a camera and a plumbline. I should indeed be happy to think that these few remarks might lead to an extension of these observations by many others than myself, who would, I am confident, find such study a subject of interest.

I wish to thank many friends and collaborators for their help in this investigation, and in particular Professor Amoroso for the loan of the radiogram of the mouse's skull, Professor Cave for the gift of skulls and help in dissection, Mr. F. J. Pittock, A.L.S., for photographs, Mr. P. Venning for radiograms, Miss E. R. Turlington for drawings, and Mr. H. Barker and Mr. H. C. Bartle for laboratory assistance.

ADDENDUM.

Since delivering the Address printed above, I have had the opportunity of seeing the work of L. Girard, "*Port habituel de la tete et fonction vestibulaire*" (Mammalia, Paris, mars-juin 1947), in which the author develops the views expressed in his earlier paper. He states, and I have no doubt that in the case of many animals, he is correct, that at normal positions of the head the plane of the lateral semicircular canal is horizontal, but he presents no evidence in the form of photographs of live animals against a plumb-line that this is so.

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ADDED COMMENT (not in the original paper)

T.D.M. Roberts, in his state-of-the-art book, "*Neurophysiology of Postural Mechanisms*", questions de Beer's conclusions about the 'normal' position of the head in humans, as perhaps he should because many, if not the majority of, people hold their heads habitually pulled back in a manner that interferes with their coordination and freedom of function.

Roberts writes on page 227 of the 2nd edition of "*Neurophysiology of Postural Mechanisms*" (in an atypically poetic style):

> "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 specials of mammals and for 20 species of birds, each animal characteristically carries the plane of its 'horizontal' canal very nearly parallel to the horizon. 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 of 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[i] into the horizontal position gives the head the unnaturally elevated attitude of a military parade."

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[i] Note by DG: The "*anthropometric reference plane*" referred to by Roberts above is the so-called Frankfort plane mentioned by de Beer in this article: "*the plane which passes through the lower border of the eye-socket and the upper border of the external auditory meatus*" [the external ear hole].