On The Role of Gravity in Human Spatial Orientation

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THE MOST IMPORTANT sensory systems giving us information on our position in space are the visual, the tactile, and the static receptor organs. As static receptors we designate those responding to gravity and to comparable mechanical field forces. In vertebrates this means particularly the statolith organs of the labyrinth. The participation of these organs in the spatial orientation of normal human beings has been well established.[4, 21, 22, 30] We need only recall that under circumstances where tactile and visual cues are largely absent, persons with labyrinth damage are often disoriented: they are unable to keep the body balanced when standing on one leg with eyes closed. And diving is very dangerous for such persons because they cannot find the surface without optical cues, in contrast to intact individuals.[21]

The solution of the old problem as to how the statolith organs of the vertebrates operate, seems to be the shear principle.[2, 3, 4, 17, 27] Humans, too, follow the same pattern, as far as our results show. As indicated in Figure 1, the weight of the statolith can be resolved into a pressure or pull component acting perpendicular to the sensory epithelium, and a shear component acting parallel to it. The shear is given by the product m.f. sin α, that is, the mass of the statolith (m) times the strength of the mechanical field (f) times the sine of the angle of inclination (α), the angle by which the animal or the organ in question is tilted out of zero position. Since the mass of the statolith remains constant, the shear changes proportional to f. sin α. As v. Holst showed in his fish experiments,[17] the sense organ is stimulated exclusively by the shear component.

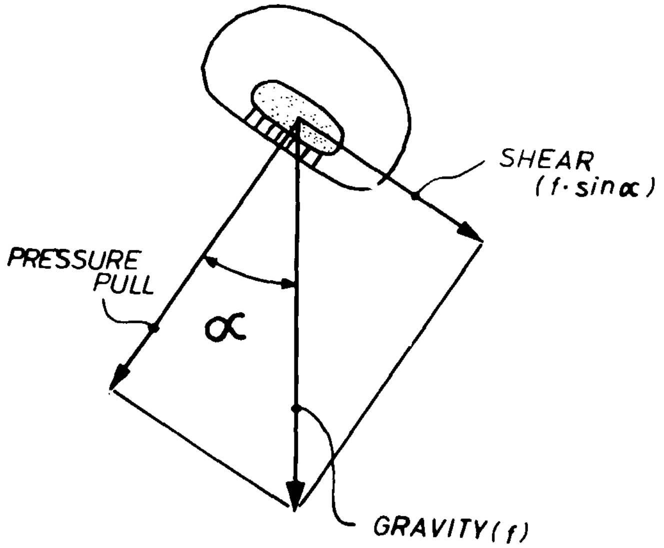

Fig. 1. Schematic diagram of statocyst showing the gravitational force (f), acting on the statolith, resolved into two components, pressure or pull (perpendicular to the epithelium) and shear (f•sin α, paralell to the epithelium).

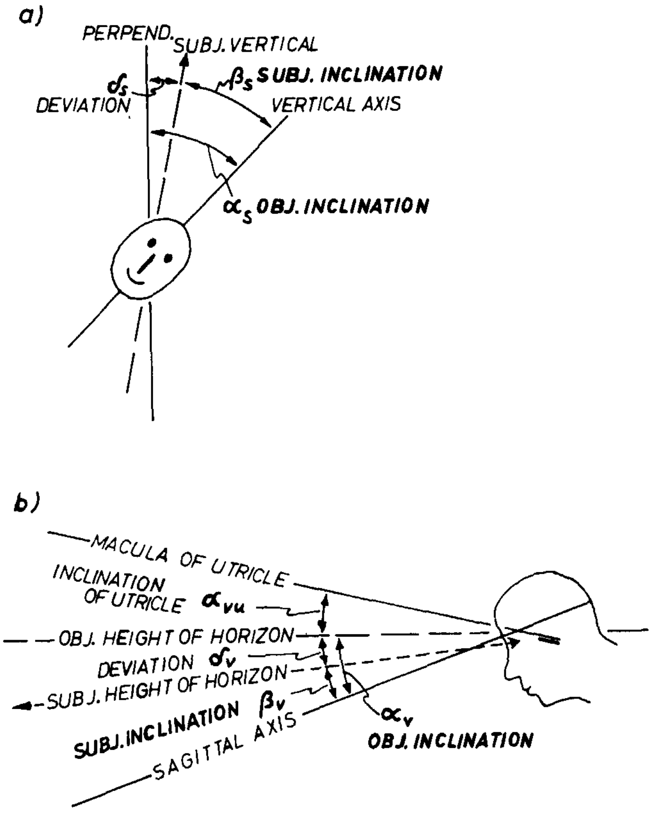

Fig. 2. Designation of the various parameters used in investigation of the subjective space coordinates: a) in tilting the body sideways (roll), and b) in turning the body (or head) fore and aft (pitch). [The sketch a) also demonstrates the Aubert phenomenon.]

All other linear acceleration forces naturally act in the same way as gravity. This explains the fact that persons exposed to centrifugal forces in addition to gravitational ones—on a rotating surface or during turning maneuvers of an airplane—experience a tilting of their surroundings, although their actual orientation relative to gravity remains unchanged.[5, 16, 13, 20, 21, 22, 26, 28, 31, 33, 38] Graybiel designates these perceptual phenomena [15]—the apparent displacement of objects in space—as the oculogravic illusion. These effects had hitherto been explained solely on the basis of the

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Modified form of a lecture given at the meeting of the "Deutsche Gesellschaft für Luft—und Raumfahrtmedizin," Oct. 1963 in Munich.

This paper is dedicated to W. v.Buddenbrock on occasion of his 80th birthday and to his memory.

changing direction of the force field. But the shear theory postulates that the strength of the field must also have an effect. For the same reason the gravity receptors must also respond, when an astronaut in his space capsule is exposed to the acceleration of blast-off, or when this acceleration stops at cutoff. Sensations which can be explained by such stimulus effects are in fact known from manned orbital flights.

One method of studying spatial orientation and its dependence on the function of gravity receptors lies in the investigation of the so-called *subjective* or *perceived* vertical and other subjective space coordinates (definitions of parameters, see Fig. 2).

Subjective Vertical During Lateral Tilting Under the Influence of 1g and 2g:–In a given laterally tilted position, say 30°, in some cases the subjective vertical will often be set somewhat closer to the subject's head axis than the true vertical; this deviation is called Aubert phenomenon (see Fig. 2a). In other cases, at the same inclination of 30°, the subjective vertical can be set on the other side of the true perpendicular. This type of deviation is called Müller phenomenon.[23] The term Aubert phenomenon means that the perceived inclination (angle β_s) is smaller than the actual inclination (angle α_s), the term Müller-phenomenon is the reverse. Since their discovery by Aubert in the last century, these phenomena have been studied, both from their psychological aspect and from that of sensory physiology.[9, 10, 23, 38, 39] We have concentrated our attention on the sensory and the central nervous mechanisms.

Method:–The experimental subject lies strapped to a board (Fig. 3a). His head is tilted sharply back so that the vertical axis of the head is approximately vertical. The subject can be rotated about the horizontal axis, thus bringing the head into various laterally tilted (rolled) positions. In front of him the subject sees a luminous line, which he adjusts to correspond with his subjective vertical by means of a knob. The whole apparatus is contained within the capsule of a centrifuge (Fig. 3b). In operation the capsule swings into line with the resultant of the two forces acting on it. For the experimental subject, therefore, the direction of the force field remains *constant* relative to his surroundings, and only its strength (the number of g) changes.

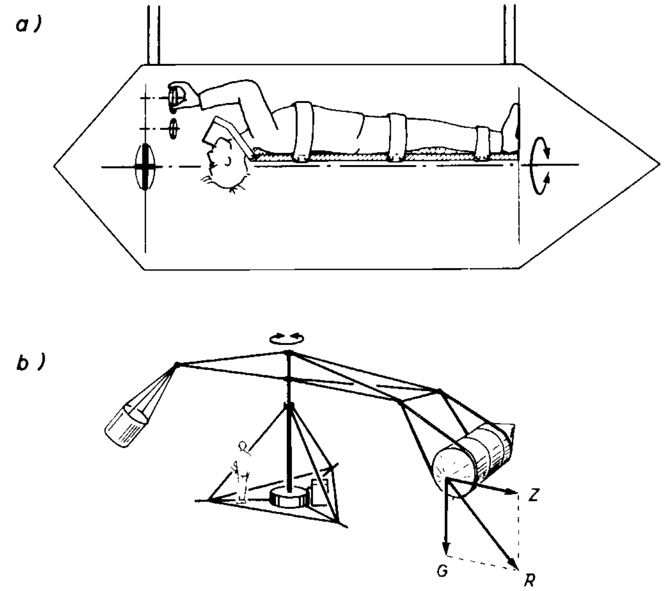


Fig. 3. a) Experimental setup for measurement of the subjective vertical in the capsule of the centrifuge. b) Schematic drawing of the centrifuge in motion; G gravity, Z centrifugal force, R resultant force.

Figure 4 shows the results of experiments, performed under the influence of 1g and of 2g. The perceived inclination is shown as a function of the actual inclination. Perfect compensation, that is perfect agreement between actual and perceived inclination, would give a diagonal line. The curve of 1g lies below the diagonal. Thus the perceived inclination is less than the actual one (Aubert-phenomenon). The curve flattens out above, and then bends upward again at inclinations beyond about 120-150°. Later on we will take a closer look at this part of the curve, representing inclinations in which the head hangs downward. The curve for 2g gives the results of the experiments in which the experimental subject is exposed to twice the normal gravitational force. The initial portion of the curve, up to about 90° inclination, shows the Müller-phenomenon. The curve rises much more steeply than the curve for 1g. At about 30° of tilt, for example, a perceived inclination of over 40° was recorded, while at 1g the value was only about half as large.

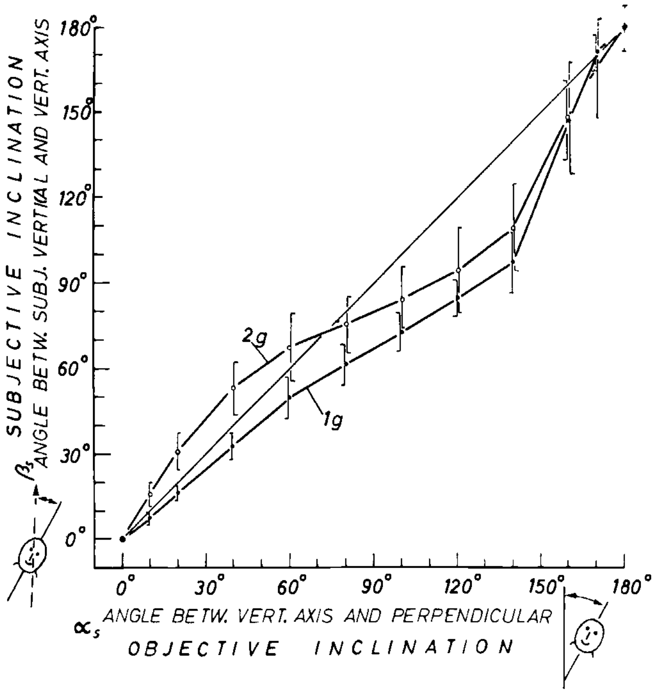


Fig. 4. The perceived inclination (β_s) as a function of the objective inclination (α_s) under the influence of 1 g and 2 g (one subject). The brackets indicate the threefold standard error (3 SE).

These experiments show that the perceived inclination increases with the strength of the force field. This increase involves a change from Aubert deviation to Müller deviation. Thus the deviation phenomena can be modified by changes in field strength. As will appear later, these measurements also permit conclusions about the functioning of the statolith apparatus.

Subjective Vertical During Lateral Tilting Under Water:—In the experiments just described, the possible effects of visual orientation were excluded, since the subject saw only the freely adjustable luminous bar. Not excluded, however, was the possibility of an influence of tactile orientation. For instance the force and the direction of the body weight acting on the board, might provide accessory information about the position in space. To reduce such effects, we tested some subjects under water.

Method:—The position of the experimental subjects was similar to that in the preceding experiments, but the body was unconstrained in a horizontal position under water, anchored only at the head and feet. The head was tilted back, the teeth clamped into a bite board, and the feet hung in the straps of a foot board. Air was supplied through a tube in the bite board. In a similar way as in the foregoing experiments, all inclinations from 0-180° were investigated.

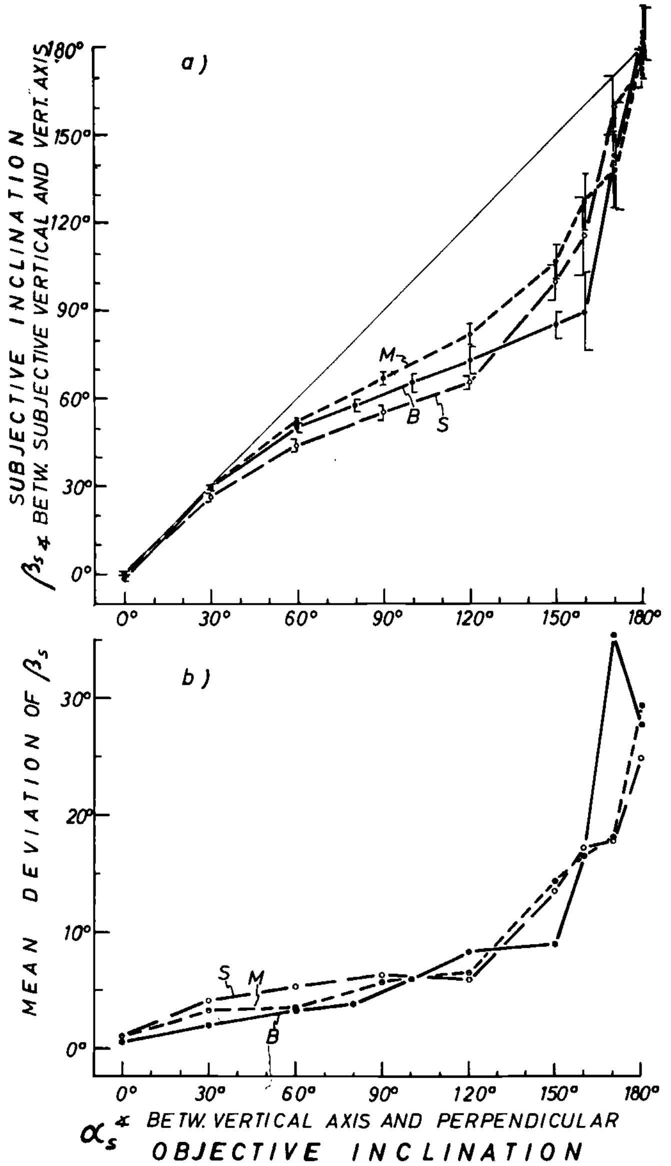


Fig. 5. The subjective inclination (β_s) as a function of the objective inclination (α_s) under water measurement (three subjects: B, M, S). a) The subjective inclination (β_s); the brackets indicate the threefold standard error. b) The mean deviation $\left(= \frac{\Sigma (M-x)}{n} \right)$ of β_s; M mean, x single deviation from mean, n number of tests.

Result:—The course of the curve (Fig. 5a) is similar to that shown in Figure 4 for 1 g. The precision with which the person perceives the vertical is also an interesting feature of these experiments. Beyond the 90° position the experimental subjects became increasingly uncertain in perceiving their position. The subjective vertical was not as well defined as in the normal head upright position. This phenomenon showed up in the scatter of the measurements: We calculated the mean deviation for each position (Fig. 5b). The range of deviation is very small for the normal upright position, it increases gradually up to 120° tilt, and from there on very sharply. In the positions of the head-down region the range of possible positions of the subjective vertical extends about to 30°.

When the head points exactly downwards, that is at 180° of tilt, the perception of the vertical may show instability phenomena. The experimental subject may imagine the upward direction of the vertical pointing from the chin to the crown of the head, and thus opposite to its actual direction. This perception can snap over into its opposite, the subjective upward direction points from crown to chin, and thus coincides with the actual upward direction.

Discussion:—From the coincidence of curve 1 in Figure 4 with the curve of Figure 5a it can be concluded that in the investigated situation the establishment of the subjective vertical and thus the perception of position is almost exclusively determined by the activity of the statolith organs and is influenced only to a very small degree by other sensory clues.

Our results show a very poor determination of the subjective vertical in the head-down position (Fig. 5b). This confirms the findings of Brown,[6] who describes a particularly poor orientation in these positions. Brown investigated persons under water, who had to indi-

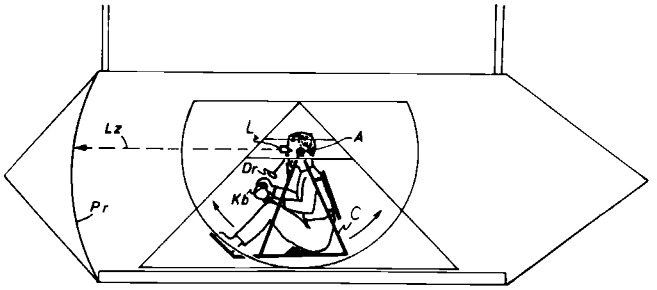


Fig. 6. Experimental setup for measurement of the subjective height of horizon and related parameters in the capsule of the centrifuge. A turning axis of the chair; C chair; Dr turning knob for moving the lamp up and down; Kb handle for turning the chair; L lamp producing the beam of light and the spot of light; Lz lightbeam; Pr screen on which the spot of light is projected.

cate the upward direction by pointing with the arm. Informative in this context are also the reports of tests performed under conditions of weightlessness, attained for short periods in parabolic flights.[11, 12] The subjects describe feelings of floating or swimming on their backs or with the head down. As these results indicate, the positions perceived under weightlessness are similar to those perceived under normal gravitation in the head down posture. One can thus suppose that in this position the stimulating effect of gravity on the statolith organs is very much less than in the normal head up position.

Height of the Subjective Horizon as a Function of the Field Strength:—In these experiments the perception of position was investigated when the subject was tilted forward or backward (Fig. 2b).

Method:—The experimental subject sits in a chair, mounted so as to rotate about an axis running through the labyrinths of the subject (Fig. 6A). A lamp projects a small luminous spot in front of the subject, who can move it up and down. In the first series of experiments the subject is put in different positions. In each position he must set the spot on the horizon, that is he must move it up or down until he sees it at eye level. The subjective or perceived tilt is then given by the angle between the direction of this subjective horizon and the sagittal axis (definitions, see Fig. 2b). In normal head posture the sagittal axis runs roughly horizontally. It has a fixed relation to the bite board plane. The bite board is a flat board connected with the chair; it is held between the subject's teeth and thus fixes the head relative to the chair. In a given position the subject was exposed to various numbers of g in the centrifuge; for each the height of the subjective horizon was determined.

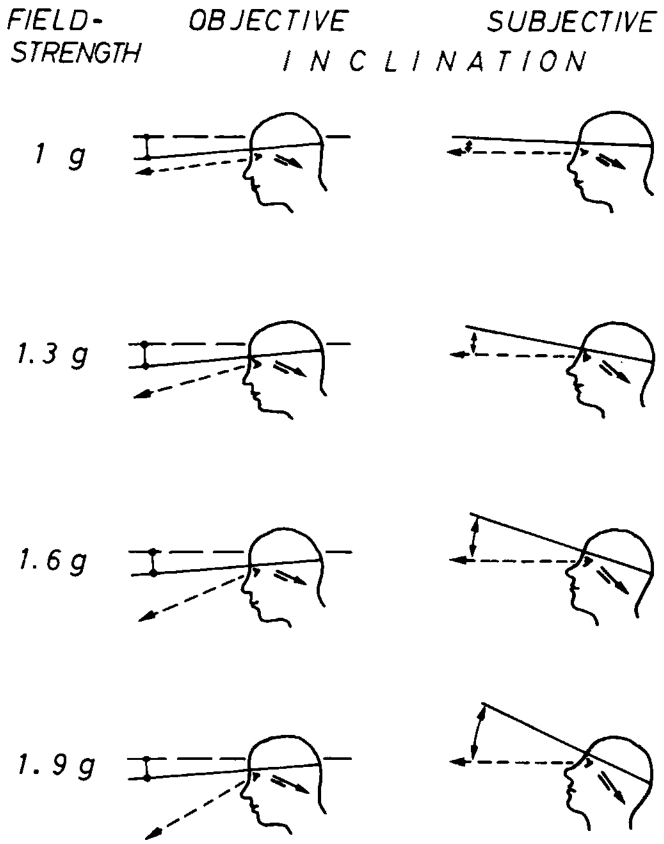


Fig. 7. The subjective inclination under the influence of increasing strength of field in a fixed objective position. ◄••• subjective height of horizon; — — objective height of horizon; — sagittal axis of head; ↓ shear in utricle. Left column of sketches shows the shifting of the subjective height of horizon with increasing g, the objective position remaining constant; the sketches of the right column show the same angular relations as in the left column, but drawn with the subjective horizon horizontally to demonstrate how the subject perceives his inclination when being tilted backwards.

Results:—Figure 7 illustrates an experiment: The setting of the subjective horizon was measured in sequence at 1 g, at 1.3 g, at 1.6 g and at 1.9 g. The left hand column shows the objective state of affairs. The subject sets the luminous spot lower each time. The right column shows the subjective state: the person has the sensation of being pitched backward more with every step of increasing g.

The result of this experiment is shown in diagrammatic form in Figure 8 in the next-to-lowest curve ($\propto_v = 5°$). The perceived inclination increases linearly proportional to the g number, it results in a straight line. The other straight lines show the results of similar experiments performed in other body positions. The more the head is tilted forward, the flatter the course of the straight line, the less is the subjective horizon influenced by the field strength. In a position with the sagittal axis about 30° below the actual horizon, the line would be horizontal (Fig. 8, $\propto_v$ be-

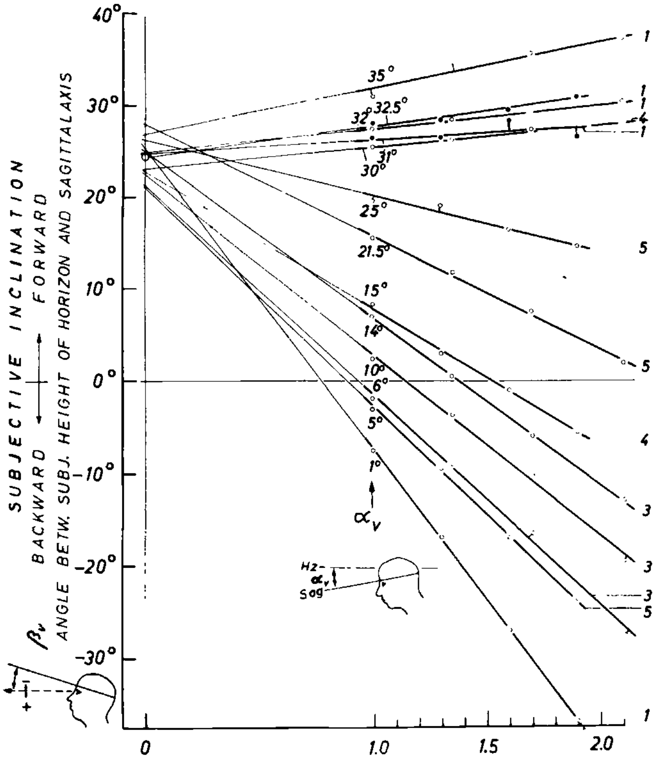


Fig. 8. The subjective inclination (β_v) as a function of the field strength in various positions ($\propto_v$). The number at the right hand border indicates the number of tests underlying the corresponding curve (one subject).

tween 25 and 30°). Thus in this head position the perception of position would be unaffected by changes in field strength.

Discussion:—In the head position just mentioned in which a change in field strength has no influence (Fig. 8, $\propto_v$ between 25 and 30°) the sensory epithelium of the utricle lies roughly horizontal, as we know from morphological studies.[7] This fact encourages the attempt to correlate our results with the function of the utricle; since the shear component is zero in the horizontal position of the sensory epithelium, a change in field strength will have no effect. To investigate this correlation for all data given in Figure 8, the shear values were calculated according to the aforementioned formula f• sin α. Then all these data were plotted as a function of the shear values (Fig. 9). Their distribution fits a straight line well. That means that the perceived inclination changes proportionally to the shear force in the utricle. This correlation between subjective inclination and shear in the utricle can be set up for the previously discussed investigations of the subjective vertical, that is of the perceived position during lateral tilting (Fig. 4). Here, too, in the region up to about 60° of tilt to either side, an approximately linear proportionality exists between perceived inclination and the shear component in the utricle. The straight line in Figure 9 can be expressed by the equation $\beta_v = k\ f \angle \sin \propto_v + O\beta'_v$. The proportionality constant k determines the slope of the straight line; it denotes the relationship between the perceived inclination (β_v) and the shear force. The straight line indicates a k of 64° g. That means that the perceived inclination increases by 64° for a shear of one g. Under conditions of normal gravity this shear is reached at $\alpha_v = 90°$. Therefore, at this actual inclination of $\alpha_v = 90°$, the perceived inclinations should only reach β_v 64°. That means there is a difference between perceived and actual inclination of 34°. Up to an actual inclination of about 55°, however, the perceived inclination (β_v) follows the actual one fairly well, for example: for $\alpha_v = 30°$ (shear = 0.5 g) we calculate $\beta_v = 32°$ and for $\alpha_v = 55°$ (shear = 082 g), we calculate $\beta_v = 52.5°$.

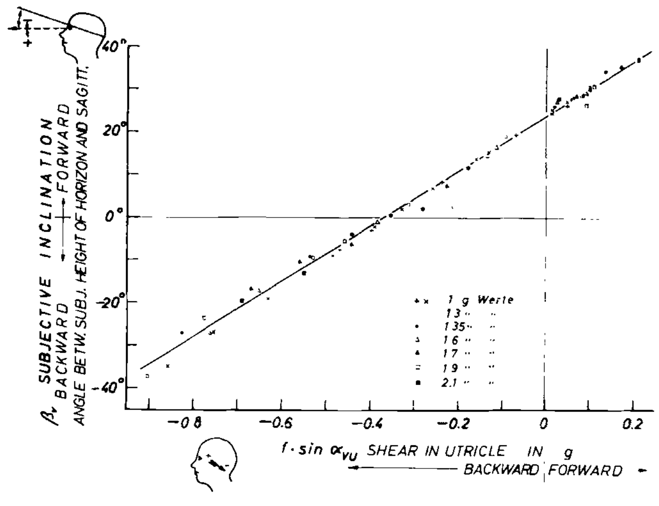


Fig. 9. The subjective inclination (β_v) plotted as a function of the shear in the utricle, calculated according to f x sin $\propto_{vu}$ from the data given by Fig. 8. The straight line is given by $\beta_v = K f \bullet \text{sine} \propto_{vu} + \beta'_v$; here K = 64 degrees/g and $\beta'_x = 24°$.

The difference between the perceived and the real inclination which begins at about 55° inclination is the analogue to the Aubert phenomenon described above for the perception of lateral tilt: the perceived inclination is smaller than the real inclination, and the difference increases with increasing inclination. In both cases—in the lateral tilting and in the fore-and-aft tilting—these phenomena are based on the fact that the subjective inclination corresponds to the shear and thus does not increase with the angle but with the sine of the angle of the real inclination. The difference between the angle and the sine of the angle leads to the deviation phenomena with increasing inclination.

The results expressed in Figure 8 allow us to make certain predictions about the consequences of the position of a pilot in his space capsule. The accelerations associated with the blastoff and cutoff of the engines during the starting and landing maneuvers will cause a very strong effect when the head is tilted backward, as is the case when the pilot lies on his back. Our results lead to the conclusion that this may result in disturbances in the spatial orientation: it changes the perceived position.

The NASA reports of the manned orbital flights contain some remarks[25] which can be interpreted in this direction. The pilots describe a feeling of falling forward when the propulsive acceleration stops. Explanation: the backwards pull of the statolith suddenly ceases, the statolith is shifted forward in a similar manner as in a subject who is raised from a backward to an upright position under normal gravity. If the position of the pilot were such that the head were inclined a little forward from the normal

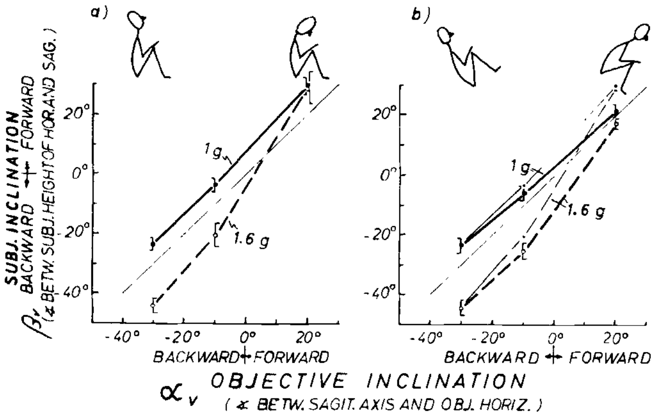


Fig. 10. The subjective inclination (β_v) as a function of the objective inclination ($\propto_v$) under 1 g and 1.6 g; the brackets indicate the threefold standard error (one subject). a) inclination of the head only. b) Inclination of the whole body; for purposes of better comparison of the curves of a) are also drawn in b) with thin lines. When the head alone is tilted forward the subject perceives 8°-11° more inclination than when the whole body is tilted; this difference decreases with increasing backward inclination.

upright position so that the utricle lay perpendicular to the direction of movement of the space vehicle the change of acceleration could not have this effect. Thus the customary horizontal position of the pilot is particularly unsuitable with respect to orientation in space.

Height of the Subjective Horizon During Tilting of the Whole Body, of the Head Alone, or of the Trunk Alone:—In the experiments described thus far the body was tilted as a whole. We performed other experiments in which the effects of tilting the body, of tilting the head and of tilting the trunk were compared.

Results:—The perceived inclination was measured as a function of the actual inclination at 1 g and at 1.6 g (Fig. 10). Figure 10a shows the experiments in which the head alone was tilted, Figure 10b shows those in which the body was tilted as a whole. The results of the latter correspond to the experiments described in the previous section. They confirm the findings shown in Figure 9: $\beta_v \backsim f \sin \propto_{vu}$. The position of zero shear would be reached at about $\propto_v = 30°$ when the sagittal axis lies about 30° below the horizon, because at this point the curves of 1g and 1.6 g coincide. Both experiments have the following in common (Fig. 10a and 10b): at 1 g the curve inclines with an angle of about 45°, as can be seen by comparing with the 45° diagonal drawn in the figures. Thus the perceived inclination changes in proportion to the actual inclination, and the position in space is perceived approximately correctly. At 1.6 g, in contrast, the perceived inclination changes much more rapidly than the actual position; the curve runs far below the 1 g-curve. So much for the agreement between Figures 10a and 10b.

The difference between the two experiments is as follows: In Figure 10a, in the forward tilted position both the 1 g and the 1.6 g curves lie higher than in Figure 10b. The position of the head in space is the same in both experiments, but in Figure 10a the trunk is bent forward with respect to the head. This results in 8-11° more perceived forward inclination than when the head-to-trunk position is normal.

In a third series of experiments the trunk was moved underneath the head which was held motionless in space by the fixed bite board (head position: sagittal axis 13° above the objective horizon). The trunk position ranged from 30° backward to 25° forward divergent from the normal head-to-trunk posture. When the trunk was passed through these 55° from the backward to the forward position the subjective height of the horizon moved upwards by approximately 8° (under 1 g: from 1° to 9° above the objective horizon; under 1.6 g: from 16° to 8° below the objective horizon). That means that in the forward position of the trunk the subject perceives about 8° less backward inclination than in the backward position. That is to say, the subject perceives a relative forward bending of about 8°, when the trunk position is altered about 55° against the head, from backward to forward.

Discussion:—Under the influence of a higher field strength, the proportion between objective and subjective inclination is changed, when the head-position in space is changed. Not only when the whole body (head and trunk) is tilted but also when the experimental subject actively moves his head does the increased number of g cause a deviation of the perceived position from the actual position, according to the function $\beta_v = f \sin \propto_{vu}$.

When the head alone is tilted, the effect of the statolith apparatus is supplemented by another. In the forward tilted position the curves differ by a certain amount. This difference is presumably caused by receptors in the neck, which record the neck posture. This conclusion is confirmed by the crucial experiment, in which the trunk is bent while the position of the head remains constant in space. The differences in the perceived inclination between the backward and the forward position of the trunk correspond to the respective differences between tilting of the whole body and tilting of the head alone. We have similar results of Fischer[9, 10] on the location of the subjective vertical when the subject is tilted sideways (only under normal gravity). The effect of the neck receptors (trunk tilted while head fixed) and of the statolith organs (whole body tilted) are simply additive, so that one obtains the same setting as when the head is tilted while the trunk is held fixed.

Retention of Perceived Position During Changes of Field Strength (Regulation of Position in Space):—It is to be expected that the position in space is regulated by feedback processes.[19, 24] As we have seen, the subjective inclination changes under the influence of increased field strength both for whole-body tilting and for (active) tilting of the head alone. This fact has been exploited.

Method:—A given position ("reference position") was prescribed: The spot of light is fixed relative to the subject's head (Fig. 6). In order to maintain his subjective orientation, the subject must hold the spot on the horizon. He can do so only by turning himself with the chair and the light spot.

Results:—When the field strength is increased the subject perceives a change in his position, accompanied by a displacement of light spot away from the subjective horizon. He corrects this apparent change in position by changing his actual position in space (Fig. 11, second and third row). The greater the field strength, the more the subject tilts forward in order to maintain his perceived position. The last column in Figure 11 shows that coinciding with this behavior the shear component in the utricle remains at a constant level.

We have performed such experiments with the same result for a whole series of different perceived positions: the sagittal axis lay in the region between 10° above and 40° below the horizontal (Schöne 1962, Fig. 13 and 14).

Discussion:—Position is regulated by a feedback mechanism, whose sensing element is the statolith organ. A given position in space causes a particular stimulation of the statolith apparatus. This value is fed back into the system and compared with the centrally present reference value. Differences between feedback value and reference value lead to corrective changes in position.

Apparent Displacement of the Actual Horizon During Movement of the Body (or the Head Alone) Under the Influence of Increased Field Strength (Loss of Space Constancy):—The orientation in space is adjusted to the normal gravitational acceleration of 1 g. During changes of position which take place in a field of increased strength the relation between perceived and actual position changes. This is the case for tilting from side to side and from front to back. This means that in perception the objective space coordinates change when the subject alters his position; in other words, the objective space does not remain constant in perception.

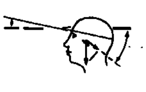
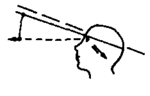
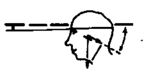
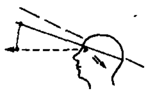
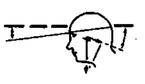
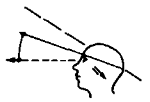
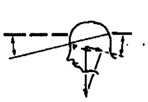
1 FIELD-STRENGTH f	2 SUBJ. INCLINATION β_v	3 OBJ. INCLINATION α_v	4 INCLIN. OF UTRICLE α_{vu}	5 SHEAR IN UTRICLE $f\cdot\sin\alpha_{vu}$
1 g			43°	0,68 g
1.3g			31,5°	0,68 g
1.7g			23,5°	0,67g
2.1 g			19°	0,68 g

Fig. 11. Compensatory changes of the objective position under the influence of increased field strength. The subject compensates for the perceived change of position in order to keep his (subjective) inclination constant. The sketches of the second column show the subjective inclination (the subjective horizon is drawn horizontally, cp. Fig. 7). The sketches of third column show the same angular relation but in the actual position in space; the arrows in the head sketches symbolize the g force and its shear component acting in the utricle. The numbers in columns four and five indicate the inclination and the shear of the utricle respectively.

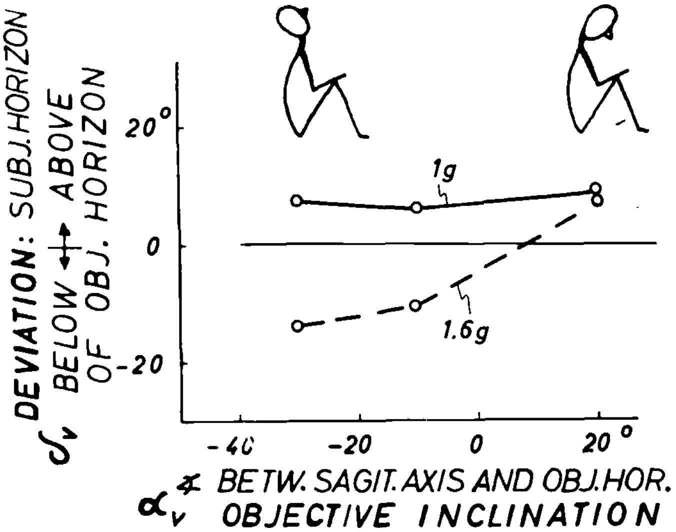


Fig. 12. The deviation (∂_v) of the subjective horizon from the objective horizon as a function of the objective inclination under the influence of 1 g and 1.6 g. Under 1.6 g the subjective horizon changes its deviation from the objective horizon when the head is tilted.

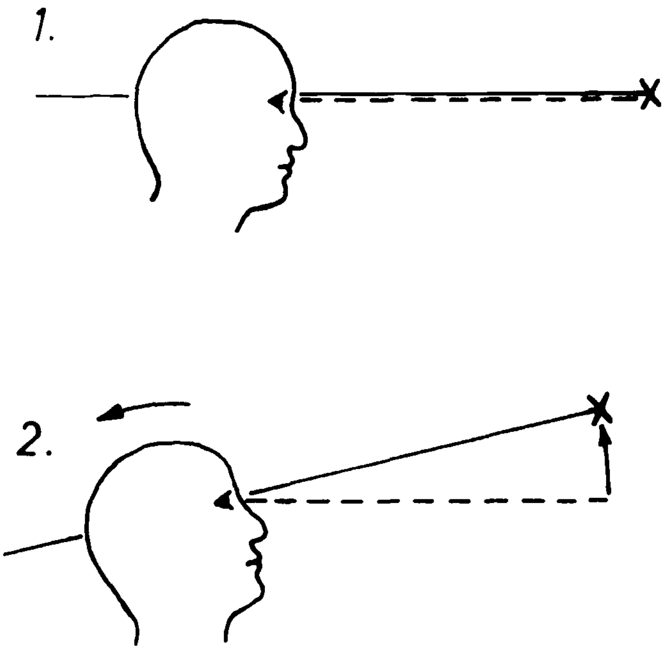


Fig. 13. Apparent movement of a horizontally fixed spot of light as a result of tilting the head under the influence of increased field strength. If the head is raised, the spot of light seems to move upwards. — — subjective horizon; —x objective horizon with spot of light.

Results:—This relationship already shows up in the results of the former chapters, for example in the second column of Figure 11. While the subject keeps its perceived inclination constant the actual horizon appears to shift upwards as the field strength is increased. Figure 12 shows this phenomenon more clearly: the difference between the real and the perceived horizon is plotted for various positions of the head in space. At 1 g when the subject tilts his head from front to back, the subjective horizon remains at about the same distance from the real one; thus the real horizon appears to remain in the same position. But at 1.6 g this is not the case: when the head is now tilted from front to back (in the diagram from right to left), the distance between objective and subjective horizon increases by about 20°. The experimental subject perceives an upward shift of the real horizon. This means: for the experimental subject the space appears to move. This state of affairs can be shown very nicely in our centrifuge (Fig. 13). When a person in the running centrifuge, and thus under the influence of increased field strength, slowly raises his head, an objectively fixed light spot appears to move upwards. The reverse occurs when the head is lowered: the spot appears to slide downwards. The same effect occurs to a lesser extent, when the subject can see a limited area of the inside of the capsule, instead of a light spot; the field of view appears to slide upwards or downwards. This does not occur in optical well-structured and extended surroundings of known space relation; here the optical orientation predominates over the gravitational one.

Discussion:—Under the influence of increased field strength, the space (represented by a light spot or by a small optical sector) appears to shift in the same direction as the movement of the head. In our experiments this phenomenon was based on visual contact, but the same effect should be demonstrable for other sensory modalities.

We repeat: under increased field strength the shift is in the same direction as the head movement. Under conditions of decreased gravitational pull, and especially during weightlessness, the opposite effect is to be expected: the light spot should shift in the direction opposite to the head movements. This presumes, of course, that only the statolith organs are functioning as sources of information, or at least that their effect predominates. Whether and to what extent the misleading infomation from the statolith receptors can be supplemented or replaced from other sources, whether for example the position receptors of the neck can play a greater role, is one of the many questions answerable by experiments to be performed under conditions of weightlessness.

SUMMARY

A. The subjective or perceived space coordinates were investigated as a function of the position of the body in the field of "gravity"; the measurements were performed under the influence of various field strengths. The subjective or perceived *vertical* was measured as a function of the lateral tilting of the body, thus by turning the body around a dorsoventral axis; the subjective or perceived *height of horizon* was measured when the body was tilted forwards or backwards (Definitions, see Fig. 2).

B. Experiments on lateral tilting:

1. The subjective inclination (= angle between subjective vertical and vertical axis of the head) was plotted as a function of the objective or actual inclination (= angle between peripendicular and vertical axis of head). In Figure 4 and 5a the curves of the tests at 1 g and at 2 g show, that from 0° to 90° of actual inclination the slope of both curves decreases and from 90° to 180° the slope increases; the shape of the curves from 0° to about 90° resemble a sinusoidal curve. In the region from 0° to 90° the 2 g curve reaches a much higher value on the ordinate scale than the 1 g curve: With increasing field strength the subjective inclination increases, and the Aubert phenomenon (=subjective inclination less than the objective one) turns into a Müller phenomenon (=subjective inclination passes beyond the objective one). The phenomena of Aubert and Müller seem to be a result of the function of the statolith apparatus.

2. The results of the measurements of the subjective vertical under water show: a) the perception of the vertical depends mainly on the function of the statolith apparatus, whereas tactile and other sensory clues seem to play no important role; b) the precision of perceiving the vertical decreases with increasing inclination: in positions in which the head hangs downwards the notion of the vertical is very vague. Accordingly the deviations of the single values from the mean increase gradually from 0° to 120° of actual inclination and rapidly from 120° to 180° (Fig. 5b).

C. Investigations of the subjective height of horizon (Fig. 6):

1a) In a normal upright position the subject feels tilted backwards when the number of g is increased (Fig. 7). This influence of the field strength diminishes, the more the head (+ trunk) position is tilted forwards (Fig. 8). At a position of about 30° forward from the normal upright position there is no more influence of the field strength; beyond this position the influence of g grows again, but in the opposite direction. b) In the 30° forward position the epithelium of the utricle lies nearly horizontally, the shear acting in the utricle is zero. If all data of the subjective inclination (of Fig. 8) are plotted against the shear in the utricle (Fig. 9) a fairly good straight line results: the subjective inclination changes proportionally to the shear force in the utricle.

2. The subjective height of horizon was measured in relation to tilting of the whole body (head and trunk) or of the head alone or of the trunk alone (against the fixed head). a) There is no obvious difference between the first two experiments with respect to the influence of the field strength: Whether the whole body is tilted or the subject tilts his head actively, for instance from back to front, in both cases at 1.6 g the subjective horizon deviates largely from the objective horizon (Fig. 10a and 10b). b) In the forward-tilted posture of the head in space the subject perceives about 8°-11° more inclination if the trunk is bent forward against the head than when the head-to-trunk position is normal. This is in accordance with the result of the third experiment in which the head was fixed in space and the trunk moved underneath the head: between the backward and the forward position a difference of about 8° was found in the subjective inclination. Neck bending receptors seem to be responsible for this effect.

3. To keep a given perceived inclination constant the subject changes its objective inclination (Fig. 11) under the influence of increased field strength. This change of position occurs in such a way that the shear force in the utricle remains constant. That means the perceived position in space is regulated by a feedback mechanism the sensory element of which is the statolith apparatus.

4. The shift of the subjective height of horizon, measured when the head (or head + trunk) is tilted under increased field strength, corresponds with the subjective sensation that the actual horizon is shifted (Fig. 12). If the head is turned backwards, a horizontally fixed light spot appears to move upwards too

(Fig. 13). That means: Under the influence of increased field strength the (optically perceived) space remains no longer constant, it moves with every head movement in the vertical plane.

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ACKNOWLEDGMENT

I want to express my thanks to Angela Seydel, Gisela Mauve and Isle Kracke for their helpful assistance in the experiments and to John Burchard, Jr. for helping me with the translation. The work was supported partly by the Deutsche Forschungsgemeinschaft.