Subjective Detection Of Vertical Acceleration: A Velocity-Dependent Response?

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SUBJECTIVE DETECTION OF VERTICAL ACCELERATION:
A VELOCITY-DEPENDENT RESPONSE?

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Abstract. Human subjective thresholds and directional sensitivity were investigated as a function of vertical linear acceleration with head erect. A hyperbolic ($r=$ 0.94) relation emerged between threshold latency and acceleration magnitude (range 0.005 to 0.06 g). This implies that detection was determined by attainment of a given *velocity* (21.6±2.65 cm/sec) rather than the acceleration magnitude *per se*. Re-analysis of previous data from horizontal accelerations conducted with head erect and supine revealed similar hyperbolic relations ($r=0.98$ in both cases) with velocity constants of 22.6±1.28 and 32.4+1.96 cm/sec respectively. From these findings it is inferred that with head erect (i.e. normal attitude re gravity) the thresholds to predominantly utricular (horizontal accel.) and saccular (vert. accel.) stimulation were similar ($P>0.7$). However, with head "supine" the saccular threshold was increased to approx. 1.5×normal ($P<0.001$). The results also confirmed a previously reported difficulty in the subjective detection of the direction of vertical movement.

Subjective orientation estimates have long been known to depend on the orientation of the head relative to gravity, with the constant feature that the *threshold* of sensitivity to gravito-intertial stimulation tends to be *least*

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when the head is held in its normal erect position (Quix, 1925; Jongkees & Groen, 1946; Graybiel & Patterson, 1955; Graybiel & Clark, 1962; Schöne, 1964). That this phenomenon is significantly dependent on the vestibular system is indicated by numerous observations. For example, the general phenomenon persists after minimizing non-vestibular somato-sensory cues through water immersion (Schöne, 1964). Again, there is substantial under-estimation of apparent tilt angle in labyrinthine-defective subjects exposed to changes of the gravito-intertial vector using the human centrifuge (Graybiel & Clark, 1965).

Since these phenomena occur in the absence of dynamic stimulation of the canals, it may be inferred that there is a significant tendency for the sensitivity of specifically the vestibular otolith organ to become progressively reduced as its orientation relative to gravity deviates from normal. Indeed, for reasons detailed in the discussion, it seems that the phenomenon is only to be expected in the light of known structural and functional characteristics of that peripheral organ and its innervations.

Taken together, these observations strongly suggest that for proper comparison of ortho-gonal (X, Y, Z) response characteristics, the head should be held in its normal erect, at-

Table I. *Dependence of detectability of stimulus and directional assessment of acceleration upon stimulus acceleration magnitude*

Step acceleration magnitude, g	0.005	0.007	0.009	0.011	0.015	0.020	0.040	0.060
% of undetected stimuli	28	17	13	13	3	0	0	0
% of wrong assessments of direction	30	28	38	26	29	23	34	28

titude relative to gravity. Experimental results meeting this requirement are available for horizontal acceleration with head erect (Travis & Dodge, 1928; Lansberg, 1954; Meiry, 1965; Niven et al., 1966; Young et al. 1966; Young & Meiry, 1968). However, although Z-axis response has been studied during horizontal movement with the subject lying down (Jongkees & Groen, 1946; Walsh, 1961, 1962; Meiry, 1965; Niven et al., 1966), there is a dearth of modern data on the threshold response to vertical stimuli with head erect (Mach, 1875).

For this and other reasons mentioned below, Malcolm & Melvill Jones (1974) attempted to measure the subjective response of normally seated (i.e. head erect) human subjects to vertical accelerative movement using a NAE (Canadian National Aeronautical Establishment) computer-controlled helicopter and later a NASA (Ames Research Center) vertical movement simulator. Interpretation of their results was complicated by the unexpected finding that, in the absence of vision, subjects tended to become confused about the direction of movement, which was not the case with Young & Mairy's subjects moving in a horizontal plane. This difficulty seems the more surprising in view of the fact that good directional information is available in both primary afferent (Fernandez & Goldberg, 1976*a* and *b,* monkey) and central (Daunton & Melvill Jones, 1973, cat) vestibular neural units responding to Z-axis (body longitudinal axis) acceleration. Furthermore associated studies of vertical eye movement (Melvill Jones et al. 1976) and spinal motoneurone excitability (D. Watt, personal communication, 1977) during sinusoidal vertical movement, revealed significant directional information in

the observed patterns of these forms of involuntary reflex response.

The present experiments set out (1) to measure normal threshold sensitivity to vertical acceleration with head erect; (2) to compare these results with those of Young & Meiry conducted in a horizontal plane and (3) to investigate further the peculiar difficulty of directional assessment referred to above. In addition, it transpired that, at least over the range of these experiments, the subjective threshold of movement could be identified with a constant time integral of the imposed acceleration, independently of the magnitude of the acceleration, suggesting that the threshold sensation was a velocity-dependent response.

Similar methods to those of Young et al. (1966) have been employed in order to facilitate comparison of results.

METHODS

All experiments were conducted on the NASA Ames Height Control Test Apparatus (HCTA) referred to above. Subjects were fixed to the seat of a blacked out cabin by a conventional aircraft restraining harness. In addition a restraining headband was adjusted to maintain head orientation so that a line joining the infraorbital margin and external auditory meatus was tilted downwards 30° relative to earth horizontal, to bring the major plane of the utricular macula close to the true horizontal. The subject wore blackout goggles behind which he maintained open eyes. The right hand was located on a light-weight, short-throw, three position switch, the mid-position

representing zero response and the up and down positions signalling a subjective sensation of the direction of acceleration. Ear muffs containing earphones permitted communication with the remote control cabin and attenuation of external auditory cues. Provision was made to use white noise for masking troublesome external sounds, but in practice this proved unnecessary.

The additional head harness also served to avoid potential accessory cues from the canals due to pitching angular movements of the head potentially induced by the vertical linear accelerations with head tilted forwards. The effectiveness of this restraint was verified by means of a small, sensitive, pitch-detecting gyroscope mounted on a dental biteboard. Test runs with 3 subjects exposed to the whole range of the experiment showed that angular head movements were usually undetectable and never exceeded ±0.5°.

The main experimental series employed 8 adult subjects with no clinical abnormality. One individual held a private pilot's licence but was not currently flying. None of the others was an aviator. They were each exposed on four occasions to each of eight magnitudes of step change in vertical acceleration. Acceleration magnitudes were all very low, ranging from $0.005\ g$ to $0.06\ g$ as shown in the top row of Table I. The distribution of acceleration magnitudes was chosen to concentrate recordings in that part of the data set where the most rapid change of response latency with acceleration was expected from the previous horizontal acceleration data of Meiry (1965). An 8×8 Latin square design permitted exclusion of learning effects and also a determination of whether practice during the experiment led to significant shortening of response latency.

All subjects were practised over the range of the experiment and informed of their performance during these runs. They were required to flick the indicator switch up or down as soon as possible after sensing the acceleration and according to the sensed direction of move-
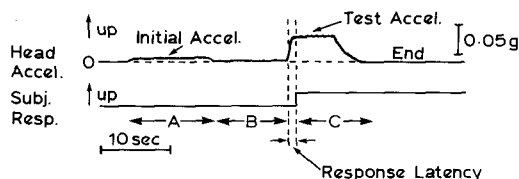

Fig. 1. Records of stimulus (head acceleration) and response (subjective response from a single test run). The initial acceleration (A) was always $0.005\ g$, either up or down. The plateau velocity (B) was always 2 ft/sec either up or down. In this example an upward acceleration of $0.04\ g$ was imposed after 10 sec of plateau velocity, and correctly identified with a latency of 1.1 sec.

ment. Practice was continued until subjects were satisfied they knew what to do.

A potentially complicating factor was static friction of the cab in its track, which could produce a detectable jolt on commencing an acceleration from rest. Consequently all test accelerations were begun at randomly chosen times after achieving a steady linear velocity of 2 ft/sec, which in turn was always attained by means of the lowest controllable linear acceleration, namely $0.005\ g$. However, since cab movement was inevitably associated with some vibration, this procedure necessitated avoidance of a simple relation between *direction* of acceleration and any sensed increase or decrease in vibration. This was achieved by balancing the occasions when a given direction of acceleration stimulus would be associated with increasing or decreasing vibration.

Vertical acceleration was recorded from two sets of linear accelerometers, one installed on the cab and a two-dimensional linear accelerometer fixed firmly to the scalp. The head mounting was arranged so that one degree of freedom paralleled the earth horizontal in a fore–aft direction when the head was tilted 30° downwards and forwards. The orthogonal axis was aligned with the true vertical. The system allowed remote checking of the correctness of head position before each run, as well as readjustment of head position in the head-harness when this proved necessary after rests between runs. Simultaneous recording of cab

and vertical head accelerometers showed that, there were no significant differences between the outputs of cab- and head-mounted accelerometer systems. Also recorded in parallel with these outputs was the subject's switch position and relevant system parameters such as the servo command voltage, safety limiting control outputs and actual cab position derived from a track potentiometer.
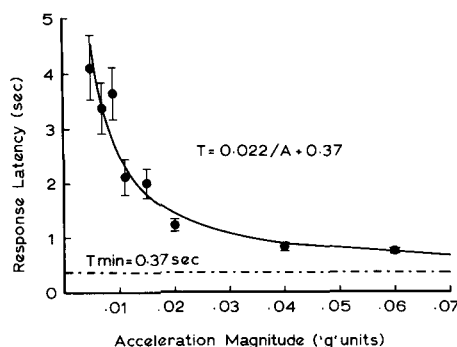

Fig. 2. Dependence of response latency upon stimulus acceleration magnitude. The continuous curve shows the calculated regression hyperbola which best fit these data. Brackets give standard error of the means ($N = 8$ subjects). T = total response latency, A = step acceleration in g units, T_{min} = calculated asymptote for the present results.

RESULTS

Threshold characteristics

Fig. 1 represents an original record obtained from a single test run. The upper trace is recorded from the vertically-oriented linear accelerometer mounted on the head. Starting from rest, there was an initial period of very low upward acceleration (A) at the standard value of 0.005 g (o.16 ft/sec²) until attainment of a steady, or plateau, upward velocity of 2 ft/sec. Then, after a randomly chosen duration of between 4 and 10 sec (B) the test acceleration was applied (upwards in this example) and maintained (C) until after the subject had registered his response by flicking the 3-way switch up or down (up in this example). The response latency was assessed as the time between initiation of the recorded test acceleration and the registration of subjective response. In practice all records were tape recorded and these latencies were measured from records played back on a suitably expanded time scale.

Fig. 2 shows the mean values of latency (±Standard Error) obtained in this way for all subjects and all runs at each of the eight acceleration magnitudes. The values shown in this figure are independent of whether the subject made a correct or incorrect assessment of direction and, of course, only those occasions when responses were indicated contribute to the curve. In practice, and as will be described below, all subjects responded on all possible occasions at acceleration magnitudes above 0.015 g. However, as shown in the middle row of Table I, and as is to be expected, progressively fewer test accelerations were detected as acceleration magnitudes decreased below this value.

The curve drawn in Fig. 2 shows the calculated least squares regression line fitted to the average latencies according to the hyperbolic relation

$$T = B/A + T_{min} \quad (\text{for } A > 0.005 \quad g) \quad (1)$$

where

T = mean measured response latency (sec); A = step acceleration magnitude (g); T_{min} = reaction time independent of A; B = slope of the regression line when plotting T against $1/A$.

The close fit of this calculated regression curve ($r = 0.94$) implies that the value of B in eq. (1) represents a meaningful constant. The important feature of this conclusion is that this constant has the dimensions of linear velocity, as is evident in the alternative form of the equation

$$B = (T - T_{min})A \quad (2)$$

From this observation the significant inference may be drawn that over the whole range of this experiment, the value B represents a consistent threshold *linear velocity* which had to be attained before generation of

a sensation of the changed movement. The calculated value of this velocity (B) for the regression curve of Fig. 2 is 0.022 g-sec (=0.71 ft/sec=21.6 cm/sec). Amongst the 8 subjects tested, the individual calculated values of B ranged from 14.8 to 27.0 cm/sec (S.D. ±5.3).

T_{min} in eq. (1) and (2) is interpreted as the constant residual reaction time for initiation of mechanical movement of the "up–down" lever after perception of changed movement. The calculated value of this residual reaction time, T_{min}, is 0.37 sec. This value is shown graphically as the dashed straight line in Fig. 2, representing an asymptotic limit of the calculated hyperbolic regression curve.

Comparison with previous "horizontal" data
In order to compare these results with the "horizontal" data of Young et al. (1966), their results have been re-fitted with "least squares" hyperbolic regression curves of the form shown in Fig. 2. In both instances, remarkably close fits were obtained, the calculated correlation coefficient, *r,* being 0.98 for both their erect and supine conditions. Also, as with the present results, meaningful values of T_{min} were obtained (0.7 and 0.6 sec respectively) although in both instances the actual values were somewhat longer than the corresponding value of 0.4 sec from our results.

Graphical comparison of results is presented in Fig. 3. Here the ordinate gives response times for subjective detection of acceleration *after subtraction of the respective minimum reaction time (T_{min}),* so that all curves begin at the same origin. The abscissa gives the *inverse* of stimulus magnitude, expressed in non-dimensional units of g^{-1}. Plotted in this way the hyperbolic relation of Fig. 2 becomes a linear one in which, according to the expression in eq. (2), the slope B numerically determines the constant velocity threshold suggested above. The figure shows calculated linear regression lines for the three sets of results. The continuous line depicts the same line as that plotted in Fig. 2 and represents the

results from the present experiment. The corresponding data from Young & Meiry's experiments conducted in a horizontal plane with subjects seated erect and lying supine are shown as the dashed line and the dash-dot-dash lines respectively.

The first notable feature is the near superposition of results for vertical and horizontal stimuli with the head held in its *normal orientation* relative to gravity. The two lines are statistically indistinguishable ($P>0.7$), the respective values of the coefficient B being 21.6 ± S.E. 2.65 and 22.6 ± S.E. 1.28 cm/sec. The close conformity of the two data sets is particularly striking bearing in mind the fact that they were obtained from different experiments using different subjects, equipment and directions of acceleration. It seems reasonable to conclude that, taken together, they represent the normal threshold of response to linear acceleration over the low amplitude range of these experiments for vertical (up–down) and horizontal (fore–aft) directions of movement.

In marked contrast, the results from Young & Meiry's subjects exposed to horizontal acceleration in a supine attitude yielded a considerably higher value of B=32.4 ± S.E. 1.96 cm/sec for the "velocity" constant ($P<0.001$). In view of considerations mentioned in the introduction as well as additional evidence discussed below, it is inferred that this difference is primarily due to the 90° deflexion of the head's Z-axis from the gravitation vertical.

Directional sensitivity
The results in Fig. 3 show that, with head erect, there was no significant difference in threshold sensitivity to low amplitude acceleration in horizontal and vertical directions. However, whereas the horizontally accelerated subjects could effectively estimate the directional component of the stimulus, Table I shows that this was not so for our vertically accelerated subjects. The upper row of the table gives the acceleration magnitudes employed in these experiments. The middle row

shows that, as expected, the percentage of *failures* to detect the *presence* of an acceleration decreased rapidly to zero as the magnitude of acceleration increased. However, the bottom row shows that the percentage of *incorrect* assessments of the *direction* of acceleration remained essentially constant at about 30%, and was therefore independent of acceleration magnitude over the entire range of experiment. Thus, in line with the previous findings of Malcolm & Melvill Jones (1974) these results appear to demonstrate a specific difficulty in detecting the direction of vertically imposed movement with the head in its normal erect position.

Additional observations

The statistical design of these experiments permits investigation of effects due to (*a*) practice, (*b*) up-going versus down-going accelerations and (*c*) increasing versus decreasing levels of vibration. None of these influences produced statistically significant effects.

DISCUSSION

Threshold sensitivity: A velocity-dependent response

An unexpected feature of the results is the closeness with which the latency–amplitude plot of Fig. 2 can be fitted by a hyperbolic curve relating response latency to the inverse of the imposed acceleration. As pointed out in Results, this implies that over the whole experimental range the perception of movement was on average first sensed only after attainment of a fixed linear velocity; B in eqs. (1) and (2). The inference is substantiated by the additional finding that re-analysis of previous results obtained in a similar way, but different circumstances, by Young et al. in 1966, yielded equally close fits to hyperbolic relationships. There seems little doubt that in all these experiments it was the attainment of a threshold velocity, rather than the acceleration *per se*, that determined the first percep-
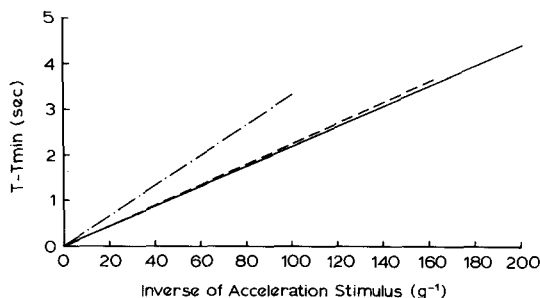

Fig. 3. Comparison of results in Fig. 2 (——) with those of Young, Meiry & Li (1966) for horizontal accelerations with head erect (- - -) and in supine position (– · – ·), after subtraction of the calculated minimum reaction times (T_{min} in eq. (1) and (2)). Note that response time in seconds (ordinate) is plotted against the *inverse* of the acceleration stimulus (g^{-1}). The lines are calculated "least squares" regression lines for each data set, with respective correlation coefficients (r) of 0.94, 0.98 and 0.98.

tion of changed movement. The finding is closely akin to that associated with the well-known "Mulder product" (van Egmond et al, 1949) for the semicircular canals. Thus the dynamic characteristics of the semicircular canals can be approximated by an integrating angular accelerometer over a wide range of brief acceleration stimuli, such that the product of acceleration and time-to-detect is a constant (1.5–2.0°/sec). However, neither direct measurement of otolith end-organ mechanics (De Vries, 1950) nor systematic analysis of identified primary afferent response (Fernandez & Goldberg, 1976*b*) point to a peripheral vestibular origin for this well defined integrative characteristic. Analysis of peripheral otolith units indicates the presence of a first order lag operator which could be associated with the mechanics of otolithic membrane displacement. However, the relevant time constant determined by Fernandez & Goldberg (median 16 ms for regular units and 9 ms for irregular units) are more than two orders of magnitude too small to account for the acceleration integration implied by the present experiment. Furthermore, their illustrations of regular and irregular unit responses to short duration force trapezoids (approximating the

present acceleration profiles) show a rapid rise in unit activity following force onset, and no evidence of any long time constant integration of acceleration in the end-organ.

This raises the important question, to what extent can the perceptual response to these very low level accelerations be attributed to stimulation of the vestibular sensory system? The matter was touched upon in the introduction, where studies were quoted in which subjective sensations of change in direction of the perceived vertical were retained after minimisation of somatosensory cues by water immersion but were impaired in labyrinthine-defective subjects. Furthermore, Young & Graybiel (unpublished) found that labyrinthine defective subjects had 8–15 times the normal threshold for detection of horizontal linear acceleration, which is similar to the earlier finding of Walsh (1961). Moreover, that the central neural vestibular response would be sufficiently sensitive to detect the low accelerations employed in these experiments is indicated by the very low thresholds ($>0.005\ g$) reported for single acceleration-dependent central neural units in the cat (Melvill Jones & Milsum, 1969; Daunton & Melvill Jones, 1973). Theoretical calculation of acceleration thresholds based upon the signal to noise ratio in the individual otolith nerve fibres are also consistent with the observed acceleration thresholds (Ormsby, 1974). Thus it seems that the very low acceleration amplitudes employed here, extending down to the absolute threshold of sensory perception (around $0.005\ g$, see Fig. 2) would be unlikely to generate detectable bodily somatosensory cues but likely to activate suprathreshold response in the specially adapted vestibular organ.

Implications concerning utricular and saccular components of response

Insofar as the above results can be ascribed primarily to vestibular stimulation, the close similarity between head erect responses to horizontal and vertical accelerations implies similar response characteristics in utricular

and saccular components of the otolith organs. Thus both the direction specificity of hair cell orientation (e.g. Spoendlin, 1966; Lindeman, 1969; Lowenstein & Wersäll 1959; Flock, 1964) and more recently the separate recording of primary afferent neurones from saccular and utricular maculae of the monkey (Fernandez et al., 1972; Fernandez & Goldberg, 1976a) show that, with head erect, horizontal and vertical movements predominently stimulate utricular and saccular end-organs respectively.

Additional results from the latter authors also have a direct bearing on the marked difference between threshold sensitivities determined in the direction of predominent saccular stimulation with the saccule in its normal (head erect) attitude and tilted 90° relative to this attitude (subject supine). The difference is seen by comparison of the continuous and the dash-dot-dash lines in Fig. 3. As stated in results, the respective slopes of these lines are 22.6 and 32.4 cm/sec, this difference being statistically highly significant. From this finding it may be inferred that the threshold of sensitivity to saccular stimulation is significantly lower when in its normal orientation relative to gravity than when tilted 90° away from that orientation. In the same context the above authors noted that saccular-dependent vestibular primary afferents responding to +Z (upwards re head) and − Z force vectors have similar steady state discharges with head erect, but the same populations have significantly different steady state values when the Z-axis of the head is horizontal. Assuming it is the differential firing rate between +Z and −Z units which constitutes the meaningful signal, then a given change of signal effected by a given acceleration would constitute a smaller proportion of the static differential signal with the Z-axis horizontal than when in its usual vertical orientation. According to Weber's principle the just-noticeable-change (i.e. threshold) would then be associated with a larger stimulus when the Z-axis was horizontal.

Assume that the ratio of minimal detectable change in firing rate (Δf) is proportional to the spontaneous rate (f_0)

$$\frac{\Delta f}{f_0} = K$$

Assume further that the spontaneous firing rate for +Z saccular units (f_{0+}) is raised and that for $-Z$ units (f_{0-}) reduced when the Z-axis is horizontal, and that the signal (μ) which must be detected is the difference between +Z (f_+) and $-Z$ (f_-) unit rates, minus the difference in their spontaneous rates ($f_{0+} - f_{0-}$). The variances of the difference in signals (μ) is the sum of the variance of the +Z and $-Z$ rates (f_+, f_-), which in turn are assumed proportional to their spontaneous rates. Consequently, an increase in f_{0+}, even though accompanied by a decrease in f_{0-}, will raise the standard deviation in the net signal, and increase the threshold for detection of acceleration for Z-axis horizontal, relative to Z-axis vertical.

Directional sensitivity

Turning to the question of our subjects' apparent intensitivity to the direction of vertical acceleration, the possibility arises that they were responding simply to some form of change of vibration. A number of features, however, suggest this is an unlikely explanation. First, if the subjective response to acceleration carried good directional information, then since the sensory signal would presumably increase with increasing acceleration magnitude, one might expect there would then be a corresponding reduction of the directional uncertainty, which there was not. Moreover, similarity between the present data and those of Young et al. (1966) over the range of experiment is too close to have been fortuitous, and yet in marked contrast to the present results, Meiry's subjects who were exposed to *horizontal* acceleration were able to detect direction with confidence.

Thus the characteristic of directional uncertainty seems to have been associated specifically with the imposition of linear acceleration in a vertical direction, parallel to gravity. This direction is the only one associated with no relative rotation of the gravito-inertial acceleration vector. Possibly, therefore, the absence of this variable is a contributory factor (Benson & Bodin, 1966; Correia & Guedry, 1966). Perhaps also the difficulty in perceptual interpretation of the central message could be associated with a difference in the "need to know" about the direction of acceleration in horizontal and vertical directions. In this connection it is interesting to note that recent results of Vidic et al. (1976) have demonstrated differences between the oculomotor reflex responses to accelerations stimulating primarily saccular and utricular otolith endorgans, despite the similarity of subjective sensitivity thresholds revealed in the present study.

ZUSAMMENFASSUNG

Subjektive Schwellen und Richtungsempfindlichkeit für vertikale lineare Beschleunigungen wurden in aufrechter Kopfhaltung untersucht. Zwischen Schwellenlatenz und Größe der Beschleunigung wurde eine hyperbolische Beziehung (r=0.94) gefunden (im Bereich zwischen 0.005 und 0.06 'g'). Dies bedeutet, daß die Schwelle eher durch die absolute Geschwindigkeit (21.6±2.65 cm/sec) als durch die Größe der Beschleunigung bestimmt wird. Eine erneute Analyse von früheren Daten von horizontaler Beschleunigung mit aufrechter Kopfhaltung in Rückenlage ergab eine ähnliche hyperbolische Beziehung (r=0.98 in beiden Fällen) mit Geschwindigkeitskonstanten von jeweils 22.6±1.28 und 32.4±1.96 cm/sec. Diese Ergebnisse zeigen, daß bei aufrechter Kopfhaltung (also in der Normalposition bezüglich Erdbeschleunigung) die Schwellen bei vorwiegender Stimulation der Utriculi (horizontale Beschleunigung) und Sacculi (vertikale Beschleunigung) ähnlich sind (P>0.7). In Rückenlage ist die Sacculus Schwelle jedoch auf ungefähr 1.5 über den Normalwert erhöht (P<0.001). Diese Resultate bestätigen die auch schon früher beschriebene Unsicherheit im Erkennen der Richtung vertikaler Bewegungen.

REFERENCES

Benson, A. J. & Bodin, M. A. 1966. Interaction of linear and angular acceleration on vertical receptors in man. *Aerospace Med 37*, 144.

Correia, M. J. & Guedry, F. E. 1966. Modification of vestibular responses as a function of rate of rotation about an earth horizontal axis. *Acta Otolaryngol (Stockh) 62*, 297.

Daunton, N. & Melvill Jones, G. 1973. Directional representation of horizontal and vertical acceleration in the neural activity of cat vestibular nuclei. *Proc Aerospace Med Ass Ann Sci Mtg* Las Vegas, p. 144. Also in "*Comparison of brainstem neural responses to vertical and horizontal linear accelerations*". Progress report to NASA Ames Research Center, p. 29, 1973.

De Vries, Hl. 1950. The mechanics of the labyrinth otoliths. *Acta Otolaryngol (Stockh) 38*, 263.

Flock, Å. 1964. Structure of the macula utriculi with special reference to directional interplay of sensory response as revealed by morphological polarisation. *J Cell Biol 22*, 413.

Fernandez, C. & Goldberg, J. M. 1976a. Physiology of peripheral neurones innervating otolith organs of the squirrel monkey. I. Response to static tilts and long duration centrifugal force. *J Neurophysiol 39*, 970.

— 1976b. Physiology of peripheral neurones innervating otolith organs of the squirrel monkey. III. Response dynamics. *J Neurophysiol 39*, 996.

Fernandez, C., Goldberg, J. M. & Abend, W. K. 1972. Response to static tilts of peripheral neurons innervating otolith organs in the squirrel monkey. *J Neurophysiol 35*, 978.

Graybiel, A. & Clark, B. 1962. Perception of the horizontal or vertical with the head upright, on the side and inverted under static conditions and during exposure to centripetal force. *Aerospace Med 33*, 147.

— 1965. The validity of the oculographic illusion as a specific indicator of otolith function. *Aerospace Med 36*, 1173.

Graybiel, A. & Patterson, J. L. Jr. 1955. Thresholds of stimulation of the otolith organs as indicated by the oculogravic illusion. *J Applied Physiol 7*, 666.

Jongkees, L. B. W. & Groen, J. J. 1946. The nature of the vestibular stimulus. *J Laryngol Otol 61*, 529.

Lansberg, M. P. 1954. Some considerations and investigations in the field of labyrinthine functioning. *Aeromed Acta (Soesterberg) 3*, 209.

Lindeman, H. H. 1969. Studies on the morphology of the sensory regions of the vestibular apparatus. In *Advances in Anatomy Embryology*, p. 1, Springer, Berlin–Heidelberg–New York.

Löwenstein, O. & Wersäll, J. 1959. A functional interpretation of the electromicroscopic structure of the sensory hairs in the cristae of the elasmobranch Raja Clavata in terms of directional sensitivity. *Nature (Lond) 184*, 1807.

Mach, E. 1875. *Grundlinien der Lehre von den Bewegungsempfindungen* (pp. 31, 32). Engelmann, Leipzig, also Bonset, Amsterdam, 1967.

Malcolm, R. & Melvill Jones, G. 1974. Erroneous perception of vertical motion by humans seated in the upright position. *Acta Otolaryngol (Stockh) 77*, 274.

Meiry, J. 1965. The vestibular system and human dynamic space orientation. Sc.D. Thesis Massachusetts Institute of Technology. *NASA CR-628*.

Melvill Jones, G. & Milsum, J. H. 1969. Neural response of the vestibular system to translational acceleration. *Proc Conf on Systems Analysis in Neurophysiology, Brainerd Minn*, Suppl. p. 8.

Melvill Jones, G., Rolph, R. & Downing, G. H. 1976. Comparison of human subjective and oculomotor responses to sinusoidal vertical linear acceleration D.R.B. Aviation Medical Research Unit Reports Vol. V p. 256: Report No. D.R. 225.

Niven, J. I., Hixon, W. C. & Correia, M. J. 1966. Elicitation of horizontal nystagmus by periodic linear acceleration. *Acta Otolaryngol (Stockh) 62*, 427.

Ormsby, C. 1974. Model of human dynamic orientation. Ph.D. Thesis Massachusetts Institute of Technology, Cambridge, Mass.

Quix, F. H. 1925. Function of the vestibular organ and clinical examination of the otolithic apparatus. *J Laryngol Otol 40*, 425.

Schöne, H. 1964. On the role of gravity in human spatial orientation. *Aerospace Med 35*, 764.

Spoendlin, H. 1966. Utra structure of the vestibular sense organ. In *The Vestibular System and Its Diseases* (ed. R. J. Wolfson), University of Pennsylvania Press, Philadelphia, p. 39.

Travis, R. C. & Dodge, R. 1928. Experimental analysis of the sensorimotor consequences of passive oscillation—rotary and rectilinear. *Psych Man 38*, 1.

van Egmond, A. A. G., Groen, J. J. & Jongkees, L. B. W. 1949. The mechanics of the semicircular canal. *J Physiol (Lond) 110*, 1.

Vidic, T. R., Barlow, J. S., Oman, C. M., Tole, J. R., Weiss, A. D. & Young, L. R. 1976. Human eye tracking during vertical and horizontal motion. *Neuroscience Abstracts* (Revised) No. 1536.

Walsh, E. G. 1961. Role of the vestibular apparatus in the perception of motion on a parallel swing. *J Physiol (Lond) 155*, 506.

— 1962. The perception of rhythmically repeated linear motion in the horizontal plane. *Brit J Psychol 53*, 439.

Young, L. R. & Meiry, J. L. 1968. A revised dynamic otolith model. *Aerospace Med 39*, 606.

Young, L. R., Meiry, J. L. & Li, Y. T. 1966. Control engineering approaches to human dynamic space orientation. *National Academy of Science Workshop on Orientation in the Exploration of Space NASA SP-115*, p. 217.

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