

## Chapter 2

# The Role of the Otoliths

### 2.1 Which Functions Do the Otoliths Fulfil?

It has gradually been recognised that the gravitational vector, primarily mediated by the otolith organs in the inner ear, is utilised as a reference by diverse systems. Besides its obvious role in the vestibulo-ocular and vestibule-spinal responses (e.g. Yates et al. 2014), it also subserves a number of systems ranging from those cognitive processes involved in spatial orientation and navigation (Wraga et al. 2000; McIntyre et al. 2001; Indovina et al. 2005; Besnard et al. 2015) to the regulation of autonomic mechanisms (e.g. Watenpaugh et al. 2002; Salanova et al. 2016).

The importance of maintaining correct spatial orientation becomes apparent in a variety of extreme sporting activities such as surfing, motorcycle racing or ice skating where it is notable that well-trained participants maintain their head in an upright position while performing their various activities (see Fig. 1.1).

With the head axis parallel to gravity, the visual surround is optimally aligned with the vertical and horizontal meridia of the retina and is thus beneficial to visual acuity and cognitive processing. This phenomenon is also reflected in the recent findings of Mast and Meissner (2004), who demonstrate that retinal images of the environment are processed optimally, i.e. with a minimum of processing time with the head in an upright position. In the absence of the otolith-mediated gravity reference, the astronaut must rely largely on the visual field for orientation (cf. Fig. 2.1).



**Fig. 2.1** In the prolonged absence of the gravitational reference during spaceflight, it is necessary for the spaceflight traveller to take reference from visual (exotropic) cues or from some internal or idiotropic vector (Glasauer and Mittelstaedt 1998)

In the meantime, an increasing body evidence demonstrates the role of the otolith afferent information in the regulation of other body functions, e.g. blood pressure (Yates et al. 1999). This effect was demonstrated by the work of Denise and co-workers (Etard et al. 2004) who demonstrated that arterial blood pressure is modulated by changes in the gravito-inertial force during parabolic flight. This work contributes to the increasing evidence of the role of otolith afferences in the regulatory mechanisms of the sympathetic nervous system, contributing to the control of vascular resistance and blood pressure. In this sense, it has been demonstrated that the afferent information from the otolith system plays a role in the maintenance of bone-muscle synergy (Luxa et al. 2013; Salanova et al. 2016; Vignaux et al. 2015).

A number of experiments have been performed that demonstrate altered spatial perception during prolonged microgravity and the nature of adaptation to the altered conditions. In one example reported by Clément et al. (2001), subjects were required to indicate their perception of tilt during centrifugation (Fig. 2.2).

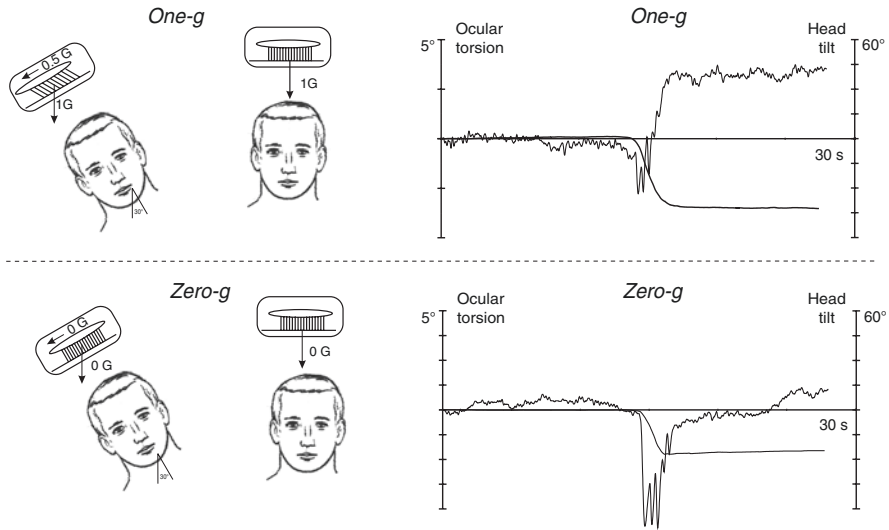
**Fig. 2.2** The short-arm centrifuge employed for the tilt-translation experiment onboard the Shuttle seen here in the training mock-up (from Clément et al. 2001)



Under one-g conditions, the tilt of the gravito-inertial vector—resulting from the additional centripetal acceleration generated by the short-arm centrifuge—was by and large correctly perceived. When performed onboard the Space Shuttle, the subjects' perception was initially very similar to that under one-g test conditions, despite the fact that the bias of the otolith-mediated gravity vector was absent. However, over the course of the 16-day mission, a gradual adaptation was observed, during which the subjective perception became aligned with the direction of the predominant centripetal acceleration vector.

Together with the subjective reports from space travellers, this demonstrates that transitions to and from microgravity radically alter the demands on sensorimotor coordination. This is reflected in the interaction between the vestibular and oculomotor systems as manifested during those head movements involving changes in orientation to the gravity vector. This is illustrated by measuring eye and head movement while tilting the head to the shoulder. Under Earthbound, one-g conditions, the otolith organs continuously signal head orientation relative to the gravity vector.

When the head is tilted, e.g. to the left, this reorientation with respect to gravity is perceived by the otolith organs, and via reflex pathways to the extraocular muscles, a



**Fig. 2.3** *Upper panels:* Under one-g Earthbound conditions, a head tilt to the left directly elicits a rapid counterclockwise eye movement to the *left*, followed by a transient burst of nystagmus beats and a static ocular torsion to the *right*. *Lower panels:* In microgravity a similar counterclockwise head tilt elicits a similar burst of counterclockwise nystagmus beats but no change in static ocular torsion occurs (from Clarke and Kornilova 2007)

compensatory rotation, or counterroll, of the eye is elicited. In contrast, when performed during spaceflight, in the absence of the gravity bias to the otolith organs, the same manoeuvre elicits no counterroll. Comparative recordings of eye and head position for a head tilt to the left, under one-g and zero-g conditions, are shown in Fig. 2.3.

Under one-g test conditions, active head-to-shoulder tilt, or rotation, stimulates not only the semicircular canals but also the otolith organs due to the reorientation to gravity. The combined canal- and otolith-mediated oculomotor response manifests as a volley of torsional nystagmus beats combined with a tonic ocular counterroll (OCR) (Fig. 2.3 upper panel). In microgravity (Fig. 2.3 lower panel), in the absence of gravity, only the transitory canal-mediated torsional nystagmus response remains.<sup>1</sup>

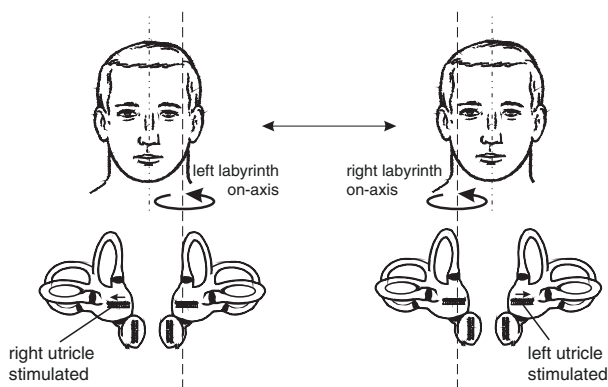
<sup>1</sup> Under both one-g and zero-g conditions, the volley of nystagmus beats commences consistently with an anticomensatory saccade. This has been observed in previous ground-based studies (Pansell et al. 2003) and can be likened to the case of the horizontal anticomensatory saccade found to initiate the eye movement response to active and passive yaw rotation of the head (Melvill Jones 1964; Henriksson et al. 1974; Barnes 1979). This is understood to be related to the intention of directing visual attention, and a neuronal substrate has recently been proposed (Roy and Cullen 2002). Whether a similar perhaps more rudimentary mechanism exists for the control of torsional eye position remains to be determined.

## 2.2 Early Spaceflight-Related Studies of Otolith Responses

The effects of exposure to microgravity on the otolith-mediated oculomotor responses have been investigated in a number of ways in previous studies (Yakovleva et al. 1982; Vogel and Kass 1986; Reschke and Parker 1987; Diamond and Markham 1988; Wetzig et al. 1990; Merfeld 1996; Clarke and Kornilova 2007). In this context, the so-called tilt-translation hypothesis was proposed after the observation was made that immediately postflight pure roll stimulation in the dark was perceived by the astronauts as translatory self-motion with only a small angular component (Reschke and Parker 1987); i.e. the CNS adapts to prolonged microgravity by reinterpreting all otolith signals to be an indication of linear translation. With regard to the functioning of the otolith organs, the asymmetry hypothesis (Yegorov and Samarin 1970; von Baumgarten and Thumler 1979) proposed that differences in weight between the right and left otolith apparatus of the inner ear are appropriately compensated on Earth, but when exposed to novel gravitational states, these compensatory stratagems become ineffective, leading to unstable vestibular responses. Testing this hypothesis, Diamond and Markham (1998) measured examined increases in OCR disconjugacy, which they interpreted as an indicator for such otolith asymmetry. This increased fluctuation of torsional eye position in their zero-g recordings could also be an indication of a stabilising, or inhibitive, role of the otolith information.

All of these previous studies lacked the methodology for unilateral stimulation to each of the otolith organs, the utricle and saccule. A unique approach to applying linear acceleration independently to the left or the right otolith organ was introduced a number of years ago (Wetzig et al. 1990). Rather than accelerate the whole body with simultaneous stimulation of both vestibular labyrinths, this approach employs unilateral centrifugation (UC) (see Fig. 2.4 and Appendix for details).

In principle this stimulus technique provides for linear acceleration along the interaural axis, i.e. predominantly across the planes of the utricles. That the right and left labyrinths are separated by approximately 7 cm permits the generation of centripetal acceleration when one labyrinth is positioned on axis on a rotator. Thus



**Fig. 2.4** Basic principle of unilateral centrifugation for the exclusive stimulation of the right respectively left otolith organs in the inner ear

the eccentric labyrinth is exposed to a centripetal acceleration along the interaural axis, while the on-axis labyrinth remains unaffected. See Appendix for details.

The refinement of this procedure as a means of evaluating the unilateral utricle function has resulted in a useful test in the clinical diagnosis of vestibular disorders (Clarke et al. 1996, 2001; Schönfeld et al. 2010; Schönfeld and Clarke 2011; Wuyts et al. 2003; Buytaert et al. 2010).

## 2.3 Recent Postflight Testing of Otolith Function

The availability of unilateral utricle and saccule testing facilitates investigation of how and to what extent the individual otolith subsystems adapt to microgravity. To this end unilateral utricle and saccule tests were performed during the preflight and postflight phases of spaceflight missions.

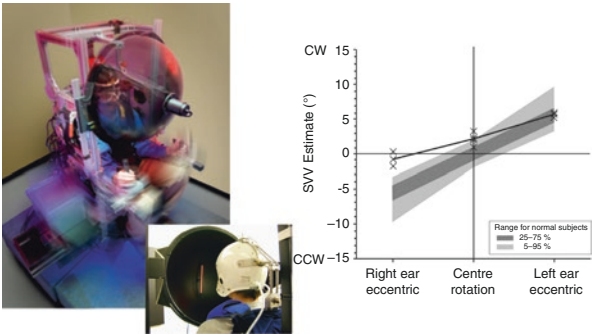
The study described here represents the first approach to comprehensive unilateral examination of otolith function with respect to the effects of spaceflight and the associated adaptation of vestibular function (Clarke et al. 2010; Clarke and Schönfeld 2015). It must also be noted that while this approach has proven useful in research and clinical settings, the influence of additional graviceptive receptors in the estimation of the vertical cannot be excluded. The existence and influence of such truncal graviceptors have been documented, above all by Mittelstaedt (e.g. 1997). The extent to which they may influence eye position or movement remains to be examined. In the past, it has often been tacitly assumed that the utricles and saccules are arranged orthogonally in the temporal bone. However, current anatomical knowledge demonstrates quite clearly the non-orthogonality of the otolith maculae (e.g. Curthoys et al. 2009). Accordingly, it is perhaps more correct to refer to horizontally polarised cells of the otolith maculae rather than the utricle and vertically polarised cells rather than the saccule. With this in mind, the shorthand terms utricle and saccule will be employed. Furthermore, the otolith system in its entirety (i.e. otoconia, peripheral neural network, central neurons plus commissures) will have over the course of adaptation to microgravity re-established symmetrical responses to those translational accelerations of the head that still occur in micro-g. Rather than a simplistic addition of left and right responses, the complex circuitry in the central vestibular system, involving excitatory and inhibitory commissure fibres, must be considered here (Markham 1989; Uchino and Kushiro 2011). It is pointed out that under these circumstances, it would be incorrect to liken the post-flight condition of healthy subjects with that of pathological loss of function. The use of cervical vestibular evoked myogenic potentials (VEMPs) as an indicator of unilateral saccule function has found widespread use in both research and clinical diagnoses (Colebatch and Halmagyi 1992; Welgampola and Colebatch 2005). Despite the recent reports that the stimuli employed induce responses not only in the otolith organs but also in the semicircular canals, the measurement of cervical VEMPs is at present the only practical approach to testing the unilateral saccule function.

2.3.1 Utricle Function Tests

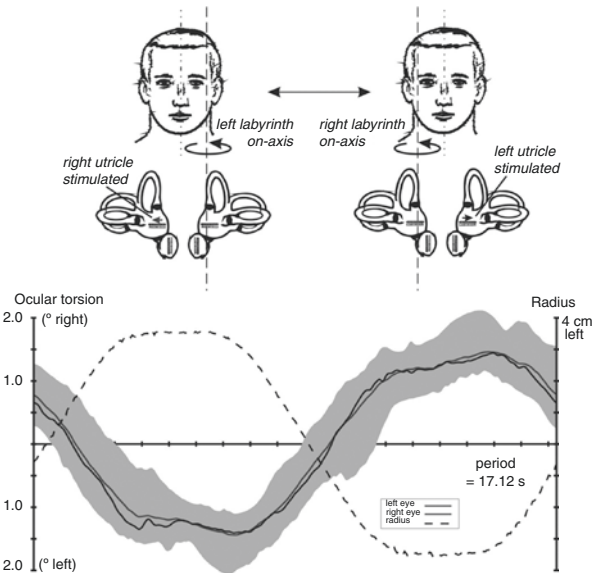
During a comprehensive postflight examination of unilateral otolith function, two approaches to testing utricle function were made, both employing unilateral stimulation (see Appendix for details).

*Subjective visual vertical (SVV)* requires the test subject to rotate a luminous line in otherwise complete darkness so that it is aligned with his/her perception of gravity (Fig. 2.5). This test encompasses not only brainstem processing of utricle signals but also those cortical brain areas required for spatial perception.

**Fig. 2.5** *Left:* Test Subject in rotating chair. The insert shows the subject's view of the luminous line in the SVV dome. *Right:* Graph showing the normal response range for unilateral stimulation of the right and left labyrinths. The test data from one patient with dysfunction related to the right labyrinth are shown for comparison



*Utriculo-ocular reflex (UOR)* test involves the measurement of ocular counterroll, induced by stimulation of the right or the left utricle and mediated directly via brainstem pathways without any involvement of higher brain functions. An example of the torsional eye movement elicited by such stimulation is shown in Fig. 2.6.



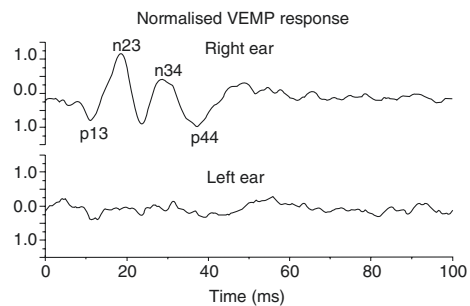
**Fig. 2.6** During unilateral centrifugation of the right, respectively, the left labyrinth elicits a conjugate ocular torsion or counterroll of the eyes

### 2.3.2 Saccule Function Test

To evaluate the postflight response of the right and left saccule, cervical vestibular evoked myogenic potentials (cVEMPs) were measured. This procedure is widely regarded and used as a clinical test of unilateral saccule function.

The VEMP provides a measure of saccular function indirectly through a vestibulo-collic reflex (Fig. 2.7). Short auditory clicks gave rise to a short-latency inhibition of activity in the contracted neck (sternocleidomastoid) muscle. The activity of this muscle is recorded with surface electrodes (see Appendix for more details). As with the UOR test of the utricles, the cVEMP is mediated directly via brainstem pathways and does not involve higher brain activity.

**Fig. 2.7** Acoustic clicks elicit a characteristic response in the neck muscles, recorded with surface electrodes on the sternocleidomastoid neck muscle. The test subject lies supine with head lifted to contract the neck muscle. The p13-n23 potential is taken as measure of response (for details see Appendix to this chapter)



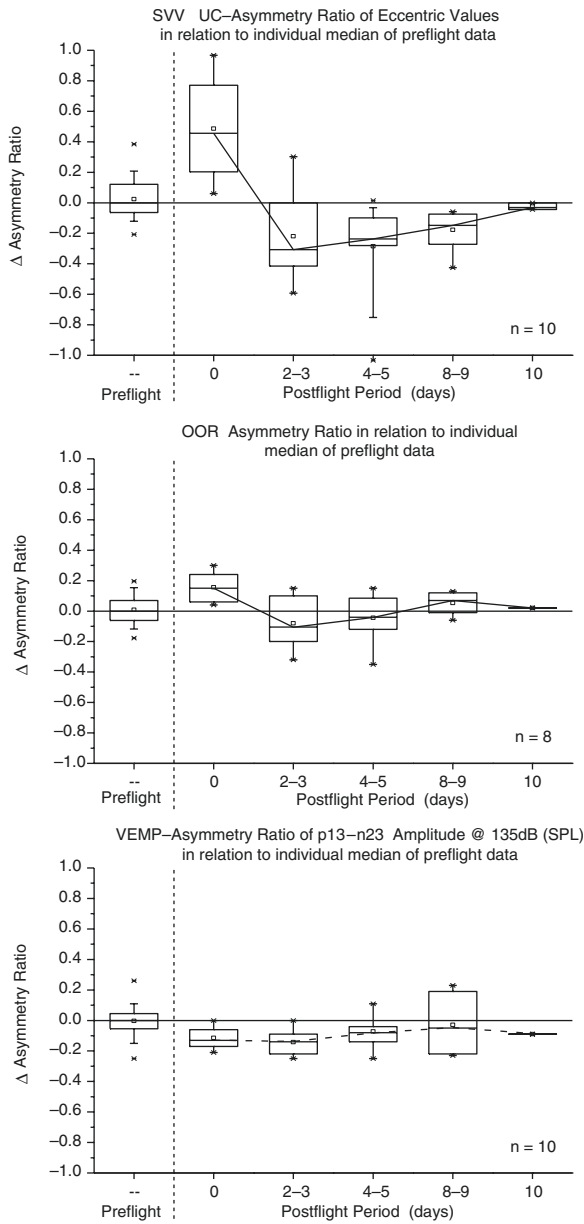
## 2.4 Related Experimental Findings

The results of the pre- to postflight tests, derived from the right-left ear symmetry ratios for subjective visual vertical, utriculo-ocular reflex and VEMPs, are summarised in Fig. 2.8.

### 2.4.1 Subjective Vertical

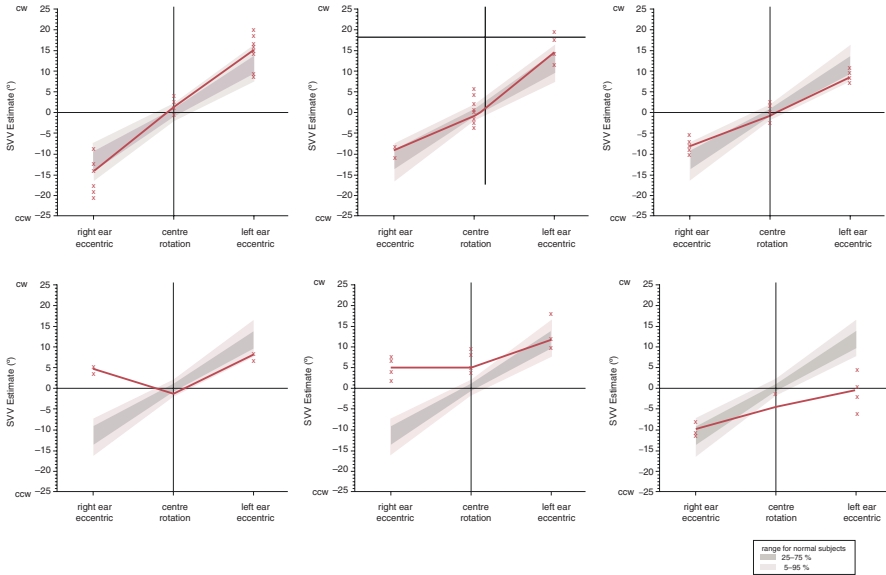
The significant shift in asymmetry on landing day (Fig. 2.8 top panel) results from an increase in those SVV estimations made during unilateral stimulation to one ear and a corresponding decrease with stimulation to the other. This relationship is inverted during day 2/3 testing where the dominant labyrinth responses approach preflight reference, while the responses from the contralateral labyrinth are clearly increased. This fluctuation dampens over the course of the 10-day postflight phase. This prolonged return to preflight values appears to take the form of a damped oscillation.

**Fig. 2.8** Longitudinal course of the asymmetry ratios for SVV, UOR and CVEMP testing over the postflight period. Distributions of the ratios for each postflight measurement session are shown relative to the preflight values (shown *left*)



2.4.1.1 Single-Case Responses

Figure 2.9 illustrates the variety of response types amongst the individuals. In the three cases shown, the postflight responses obtained approximately 3 h after landing demonstrate a clear unilateral SVV deficit, i.e. with one labyrinth testing within normal range, while the contralateral shows a clear deficit.



**Fig. 2.9** Three individual cases illustrating postflight asymmetries. *Top row*: Preflight responses, symmetrical within the normal range (*shaded area*). *Lower row*: Responses from L + 3 h, demonstrating clear asymmetries

### 2.4.2 Utriculo-Ocular Reflex

As with the SVV responses, the first postflight tests performed 3 h after landing yielded a significant asymmetry change (Fig. 2.8 centre panel). In general, testing early after landing demonstrated a significant gain increase for the right labyrinth together with a reduced UOR gain for the right labyrinth. Over the course of the 10-day postflight period, the asymmetry gradually approached preflight reference with a pattern resembling a damped oscillation.

### 2.4.3 Sacculle Function Test

The course of alteration of the asymmetry ratios is shown in Fig. 2.8 (lower panel) for a 10 dB suprathreshold stimulus. On landing day, the asymmetry ratio differs significantly from the preflight reference values. During the subsequent readaptation period, the asymmetry ratio of the cVEMP responses fluctuates in a similar fashion to the UOR and SVV responses. No consistent changes in response threshold were observed.

#### 2.4.4 *Discussion of the Findings*

The results of the utricular functional tests (UOR and SVV) indicated a consistent course of adaptation over the 10-day postflight period, characterised by a prompt increase in asymmetry between labyrinths on landing day and a subsequent reversal, tailing off to preflight baseline values after 5–8 days. The prompt increase in asymmetry observed in the early hours after re-entry demonstrates clearly the influence of the renewed exposure to Earth's gravity and supports the idea that the gain of the otolith responses is up-regulated during a stay in microgravity. Neurophysiological evidence of such up-regulation during spaceflight was reported in the toadfish (Boyle et al. 2001) on the basis of the responses of vestibular nerve afferents supplying the utricular otolith organ.

Comparison of the courses of the UOR and SVV responses clearly demonstrates the correlation between these two measures. With regard to the more pronounced response asymmetry in the SVV findings, it is noted that the UOR and cVEMP tests are based on short interneuron reflex pathways, whereas the SVV, as a subjective perceptual task, obviously involves a cognitive component that may well enhance the basic physiological signal. Comparing the time course of post-flight adaptation, the results indicate a longer time constant for SVV than for either UOR or cVEMP measures. This could be explained by the more complex neural circuitry involved in SVV estimation. All told, it appears that the brainstem functions involved adapt more quickly than the associated higher-order cognitive processes. Since it has been demonstrated that vestibular neurons are influenced by tilt-sensitive truncal receptors (Yates et al. 2000), this effect could also play a role. The increased responses measured early after landing would support the idea that otolith sensitivity, or response gain, is increased during prolonged microgravity. The findings show that after the Shuttle flight durations of on average 10 days, the return to preflight values proceeds over a period of 8–10 days. It is likely that this recovery interval would be extended after longer flights, as was observed previously in the findings on the canal-based vestibulo-oculomotor responses during and after spaceflights of 180 days in the monkey (Dai et al. 1994) and in humans (Clarke et al. 2000). With regard to the estimation of the SVV, it is argued here that the horizontally polarised cells, predominantly on the utricular maculae, play a dominant role in detecting changes of head angle relative to the gravity vector. Accordingly, in a head-upright position, any head tilt will increase their afferent discharge rate according to a sine function, i.e. most sensitive to small changes in tilt angle. In contrast, the discharge rate from the vertically polarised cell, predominantly on the saccular maculae, will change according to a cosine function, i.e. least sensitive for small changes in head tilt. The findings from SVV testing, that the response during stimulation of one utricle recovers more rapidly than the contralateral, refute the previously proposed otolith asymmetry hypothesis as the sole factor, in favour of a dominance in the CNS otolith pathways as being responsible for adaptively modifying the perception of the otolith information. The otolith asymmetry hypothesis, based on mass differences between the otoconia of the

right and left organs, cannot accommodate such a difference in adaptation. These results thus support the idea of a unilateral dominance in the utriculo-ocular neural circuitry as the primary factor rather than a morphological asymmetry as contributing to inflight and postflight disorientation.

## 2.5 Summary

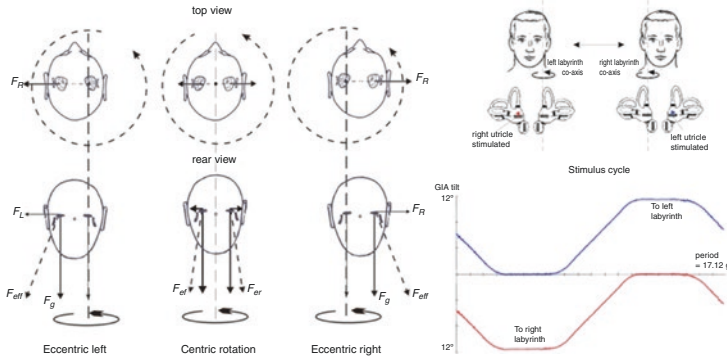
The aim of the study was to resolve the issue of spaceflight-induced, adaptive modification of the otolith system by measuring unilateral otolith responses in a pre- versus postflight design. The study represents the first comprehensive approach to examining unilateral otolith function following space flight. Ten astronauts participated in unilateral otolith function tests, three times preflight and up to four times after Shuttle flights from landing day through the subsequent 10 days. During unilateral centrifugation, utricular function was examined by the perceptual changes reflected by the subjective visual vertical (SVV) and the otolith-mediated ocular counterroll, designated as utriculo-ocular response (UOR). Unilateral saccular reflexes were recorded by measurement of cervical vestibular evoked myogenic potentials (cVEMPs).

The findings demonstrate a general increase in interlabyrinth asymmetry of otolith responses on landing day relative to preflight baseline, with subsequent reversal in asymmetry within 2–3 days. Recovery to baseline levels was achieved within 10 days. This fluctuation in asymmetry was consistent for the utricle tests (SVV and UOR) while apparently stronger for SVV. A similar asymmetry was observed during cVEMP testing. In addition, the results provide initial evidence of a dominant labyrinth. The findings require reconsideration of the otolith asymmetry hypothesis; in general, on landing day, the response from one labyrinth was equivalent to preflight values, while the other showed considerable discrepancy. The finding that one otolith response can return to one-g level within hours after re-entry while the other takes considerably longer demonstrates the importance.

## Appendix

### *Unilateral Centrifugation*

Unilateral centrifugation is performed on a rotating chair with the additional facility of shifting the test subject to the left or to the right. The UC stimulus profile consists of a spin-up with angular acceleration of  $3^\circ/\text{s}^2$  around the earth-vertical Z-axis up to an angular rate of  $400^\circ/\text{s}$ . Details of this equipment and stimulus technique have been published previously (Clarke et al. 1996, 2001, 2013).



**Fig. 2.10** *Left:* During constant angular rate rotation this stimulus technique provides for linear acceleration along the interaural axis, i.e. predominantly across the planes of the utricles. During centric, on-axis rotation, the centrifugal forces to the right and left utricles are equal and opposite. However, the right and left labyrinths are separated by approximately 7 cm, so that when one labyrinth is positioned on axis on the rotator, the eccentric labyrinth is exposed to a centrifugal force along the interaural axis, and the gravito-inertial force profile is tilted; the opposite labyrinth remains unaffected. *Right:* Unilateral centrifugation thus provides for exclusive stimulation of the right or left labyrinth. Note: the semicircular canals respond only to changes in angular velocity (i.e. acceleration). During rotation at constant angular velocity they remain silent

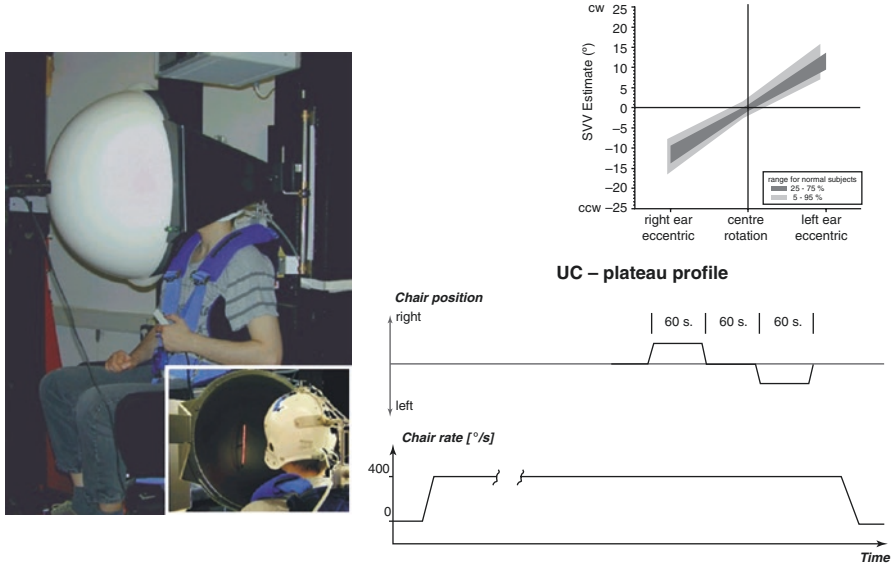
Unilateral testing is commenced after at least 2 min of constant angular rate rotation to ensure extinction of any perrotatory nystagmus or canal-induced ocular torsion (Smith et al. 1995; Buytaert et al. 2010). Translating the subject chair laterally by  $\pm 3.5$  cm from the vertical rotation axis during constant-velocity rotation then generates a centripetal acceleration to the off axis, or eccentric labyrinth of typically 0.35 g. The resulting stimulus profile is shown in Fig. 2.10 (right panel).

### ***Subjective Visual Vertical***

SVV testing is carried out in complete darkness with only a luminous line visible to the test subject, i.e. without any visual cues, and thus dependent on the information from the otolith organs for the estimation of the direction of gravity.

The SVV trials commence after the rotating chair has been accelerated (as described above), and the subject is rotating at constant velocity. Testing is usually performed with the subject in the on-centre position, where equal and opposite centrifugal forces act on the left and right utricles. Unilateral trials are then performed in the positions, left ear eccentric and right ear eccentric. The stimulus profile is illustrated in Fig. 2.11.

During the test the subject views a dimly lit red luminous line of 20 cm in length, mounted at the centre of a dome with a 60 cm diameter. The test subjects use a



**Fig. 2.11** *Left*: Subject in eccentric rotator in the Vestibular Lab. The insert shows the interior of the SVV dome with the luminous line. *Top right*: Normal SVV response range (95%). *Lower Right*: Schema of rotation and chair position profile during SVV testing

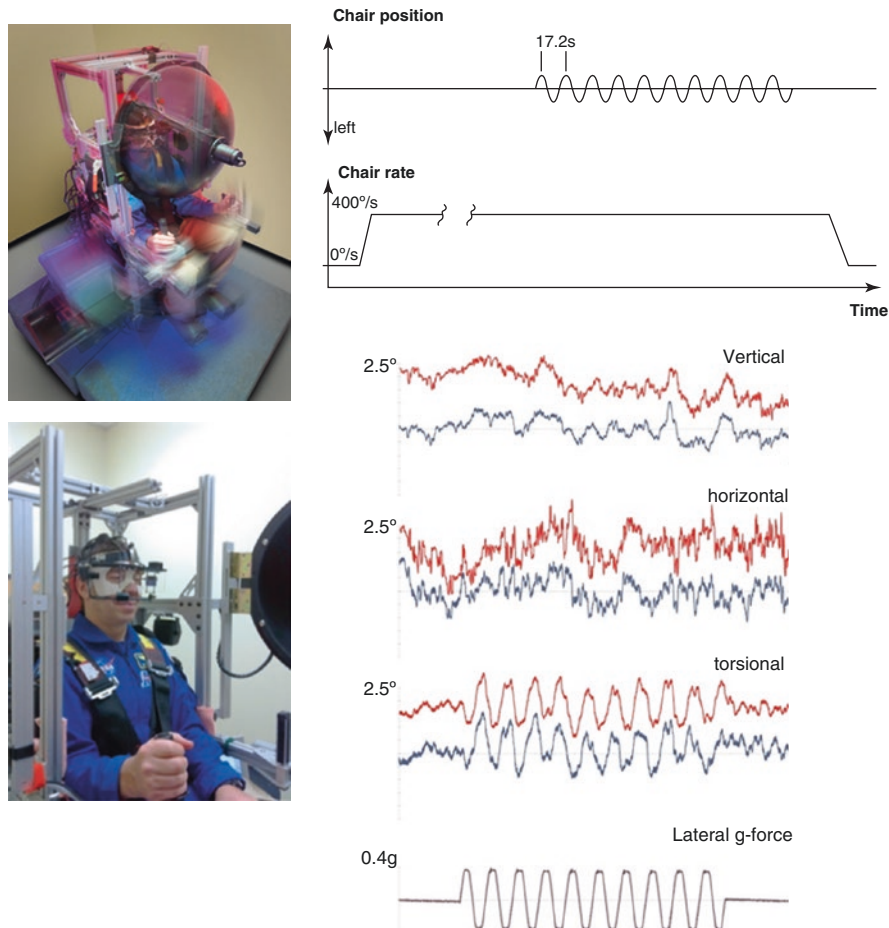
joystick to rotate the motor-driven luminous line to be parallel with the perceived gravitational vertical. Between trials, the line was extinguished and rotated to a random position under programme control and then switched on and the procedure repeated. SVV estimation was performed in each position (on-centre, left ear eccentric, right ear eccentric). The SVV asymmetry ratio was calculated from the median values of the set of trials performed in the eccentric positions.

The SVV asymmetry ratio (AR) was calculated as follows:

$$\text{SVV Asymmetry Ratio} = \frac{|\text{SVV}_{\text{right}}| - |\text{SVV}_{\text{left}}|}{|\text{SVV}_{\text{right}}| + |\text{SVV}_{\text{left}}|} \times 100$$

### ***Utriculo-Ocular Response***

During UOR testing the subject chair was oscillated from left to right. An example of one complete cycle is shown in Fig. 2.6, together with the torsional component of the eye movement response. Throughout testing, video images of the eyes were monitored, and the coordinates of each eye were recorded for offline analysis. See Appendix for details. All measurement and evaluation of eye movements were performed with the DLR Eye tracking Device (ETD),



**Fig. 2.12** *Left*: Rotating chair, insert showing astronaut wearing the ETD for recording eye movements. *Top right*: Schema illustrating the UOR stimulus profile. *Lower right*: Resultant three-dimensional eye movement response with clear modulation of the torsional component, as elicited by the stimulus to the utricle. The *two full lines* represent the torsional movement of the subject's right and left. The lower trace shows the acceleration level as measured at the subject's head

providing high-resolution and sampling-rate measurement of 3D eye movement (see Chap. 5 for details). The stimulus profile for UOR testing is illustrated in Fig. 2.12.

The measure of change in the UOR was determined by calculating the ratio of the OCR magnitude (in degrees) to the effective tilt of the gravito-inertial vector (in degrees) at the eccentric ear. The left-right asymmetry of the UOR was calculated as:

$$\text{OOR Asymmetry Ratio} = \frac{|\text{OCR}_{\text{right}}| - |\text{OCR}_{\text{left}}|}{|\text{OCR}_{\text{right}}| + |\text{OCR}_{\text{left}}|} \times 100$$

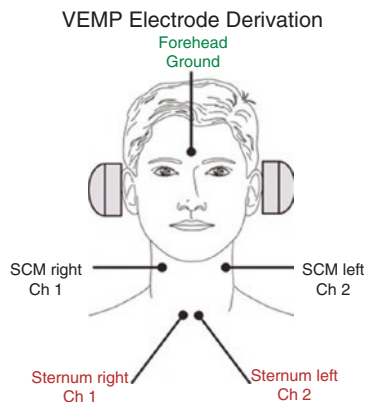
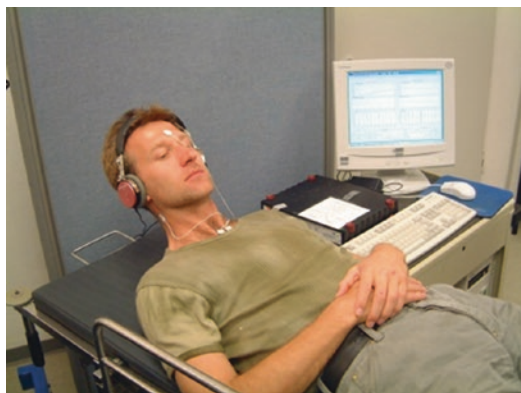
## ***Cervical Evoked Myogenic Potentials (cVEMPs)***

The VEMP provides a measure of saccular function indirectly through a vestibulo-collic reflex (Fig. 2.13). Short auditory clicks gave rise to a short-latency inhibition of activity in the contracted neck (sternocleidomastoid) muscle. The activity of this muscle is recorded with surface electrodes. Left-right asymmetry values are based on the amplitude of the response from the p13-n23 segment.

The left-right asymmetry ratio was based on the amplitude of the response from the p13-n23 segment. The normalised p13-n23 amplitudes and the symmetries of the subjects' responses are analysed using the following formula:

$$\text{VEMP Asymmetry Ratio} = \frac{|p_{13}n_{23}\text{Amp}_{\text{right}}| - |p_{13}n_{23}\text{Amp}_{\text{left}}|}{|p_{13}n_{23}\text{Amp}_{\text{right}}| + |p_{13}n_{23}\text{Amp}_{\text{left}}|} \times 100$$

During the preflight sessions, the reference data were determined for each individual: VEMP threshold—125 dB (SPL) in one subject, 130 dB (SPL) in six subjects and 135 dB (SPL) in two subjects. The asymmetry ratios all remained within the 30% range employed clinically for normal subjects.



**Fig. 2.13** Muscle activity in the neck is recorded with surface electrodes as subjects lay supine and lifted their heads to contract the neck muscle. Responses are averaged across sets of 150 auditory clicks (five clicks per second) presented during tonic contraction

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