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PARABOLIC FLIGHT REVEALS INDEPENDENT BINOCULAR CONTROL OF OTOLITH-INDUCED EYE TORSION

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INTRODUCTION

Binocular studies conducted in long-term spaceflight (10) have indicated that the torsional eye position determined in 1 G of Earth is considerably altered differentially in both eyes for the duration of six-month missions. This differential alteration, termed offset, suggests that the two eyes are separately controlled by the utricular and possibly saccular inner ear otolith organs on the two sides, which may not be bilaterally symmetrical as has been shown in the rat (30, 31). This hypothesized asymmetry is postulated to be compensated in the lifelong 1 G on Earth but is decompensated in novel gravitational states (1). Flight in parabolic aircraft offers the opportunity to explore this phenomenon more fully and to compare the responses in hypergravity as well as hypogravity to those in the 1 G state.

The parabolic patterns flown on the NASA and ESA (European) flights have similarities and differences. They are alike in achieving repeated episodes of 20-25 seconds each of approximately 1.8 G and 0 G with the transitions between the G states sometimes being quite abrupt. They are different in that NASA flies repeated smoothly linked parabolas, while ESA's paradigm consists of 1.8, then 0 G, then another somewhat irregular 1.8 G state, followed by a several minutes' pause at 1 G before the pattern is repeated. The repeated episodes of 1 G in the ESA flights have revealed aspects of the otolith-eye torsion reflex that were not apparent in our studies aboard the NASA flights (8, 9, 20).

The otolith system responds to changes in linear acceleration, e.g. gravity, and acts to regulate posture, head-on-neck relations, and to stabilize the eyeballs. The last is the task of the otolith-ocular system, of which ocular torsion is a part. The shearing action of otoconia on otolith hair cells is the effective stimulus. Compressional forces do not affect either the sensitivity of otolith afferents or their force-response relations (13).

Maximal stimulation occurs when the linear acceleration vector parallels the major planes of the otolith organs. Yet, neither the utricle nor the saccule is a flat plane, but are shallow bowl-like shapes (4), whose curved sides receive some stimulation even when the vector is perpendicular to the major plane. Response vectors on linear acceleration obtained from the superior division of the vestibular nerve are arranged in a horizontal plane, approximately in the major plane of the utricles (12-14). On the other hand, response vectors from the inferior division of the vestibular nerve are in the vertical plane, approximately in the major plane

of the saccules (12-14). In the experiments reported here, the subjects were seated upright and G was directed along the subjects' submental-vertex axes.

The otolith-ocular torsion reflex has a clear function in fish and certain other vertebrates but has a poorly understood role in humans and other mammals. Nonetheless, it provides a window to view otolith function in humans. When ocular torsion is examined in both eyes simultaneously over many parabolas, predictions can be made about the subject's likelihood of experiencing space motion sickness (SMS) (9, 20), and about the linkage between the otolith systems and the individual eyes.

METHODS

Eight subjects were tested, seven males and one female. Their ages ranged from 35 to 54 years (mean 40.4). Two were astronauts, having flown long-term missions on the MIR space station. Two others were in the astronaut pool. The remaining four were ESA employees. All gave oral and written consent, and their participation was approved by the ESA Medical Boards and by the University of California, Los Angeles, Human Subject Protection Committee.

Each subject flew 15 European-style parabolas (see above) aboard either the French Caravelle or the Russian Ilyushin test aircraft. Both aircraft were fitted with accelerometers which fed directly into our data recording system. The subjects sat in a special metal chair, fixed to the floor in the center of the airplane, facing aft. Each subject was strapped in the chair; the head was stabilized in the upright position by a preformed bite-bar. The major linear acceleration vector (G) was along the subject's submental-vertex (z) axis. A mask fitted over the subject's eyes held two small video cameras with infrared light illuminating the eyes. Vision was occluded directly in front of the subject but ambient light entered on both sides of the mask. The mask and bitebar were solidly connected to each other, and they were in turn fixed to the chair. Thus, the cameras, head and chair were fixed to each other. The chair, bite-bar and all apparatus securing the subject were manufactured by TrentWells, Inc. During the flight, the subjects sat quietly upright in the chair gazing straight ahead at an imaginary target one meter distant.

Early in fitting the subject to the apparatus, the adjustable bite-bar holder enabled the centers of the two pupils to be aligned to Earth-horizontal as determined with a spirit level. The lower margins of the irises as viewed on the dual television monitors were aligned with the bottoms of the screens. Once this position was achieved, the bite-bar was locked in place. During the course of the parabolas, the eyes were repeatedly checked for any displacement, but none was seen inflight or in later off-line analysis. Synchronized data of 25 images per second for both eyes was collected on videotape, using apparatus manufactured by SensoMotoric Instruments, GMbH. All eight subjects performed well and completed the specified 15 parabolas successfully. Occasional blinking or horizontal gaze displacement of the eyes caused data from 2-3 parabolas on two subjects to be lost.

Postflight analysis took place at our UCSB laboratory.

RESULTS

Three main findings can be described: (1) Offset of the torsional position of the eyes in the 1 G state between parabolas. (2) Ocular torsion in response to novel G states. (3) Disturbances of torsional conjugacy induced by 1.8 G and 0 G.

1. *Offset of the torsional position of the eyes in the 1 G state between parabolas.*

Offset is defined as the torsional displacement from the baseline position determined prior to the onset of the first parabola, occurring in the 1 G portions of flight between individual parabolas.

Offset was clearly seen in five of our eight subjects. It typically began in the first parabola, appearing after the abrupt transition to the 1.8 G or 0 G episode and was typically greater in one eye than the other. Figure 1 shows the first parabola of subject R.T. Prior to the first parabola, the G state in the aircraft showed some fluctuation (see upper recording), and the torsion in the two eyes (lower recordings) was somewhat irregular but conjugate. The first 1.8 G period induced a modest clockwise (CW) rotation of the left eye and no change in the right eye. The first abrupt episode of 0 G caused two changes: a counterclockwise (CCW) rotation of the two eyes, with a more extreme response in the left eye. The left eye was unchanged by the next 1.8 G episode, persisted in the subsequent 1 G, and continued for the next several minutes at 1 G (not shown). The offset of one eye in 1 G continued in this and other subjects across several more parabolas, although fluctuations in response to the marked changes in G might be superimposed. In

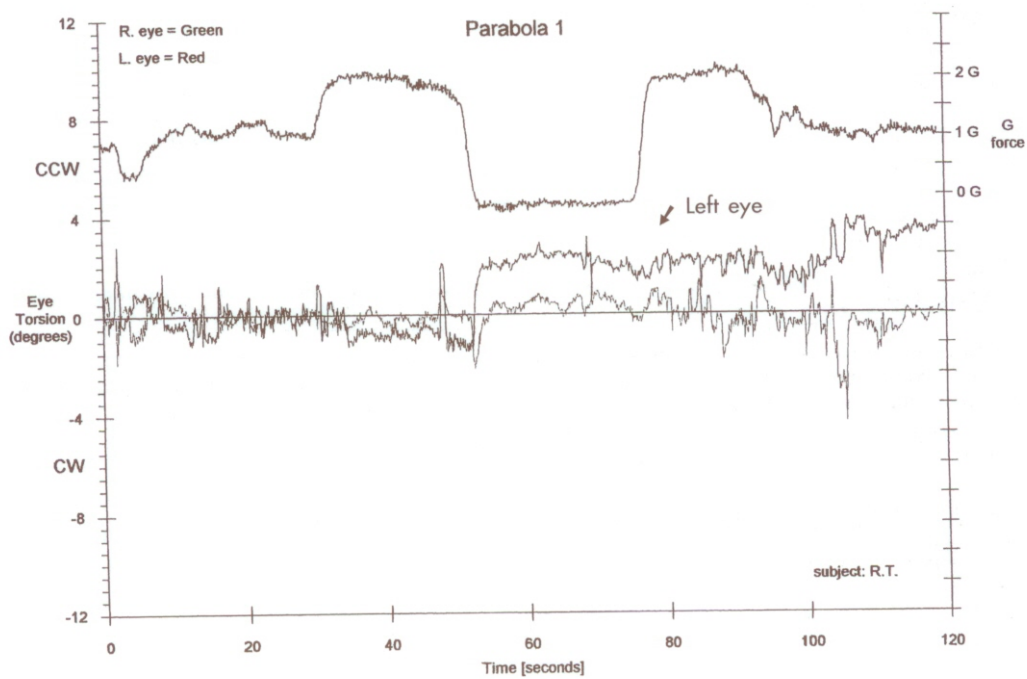

Fig. 1. - *First parabola of subject R.T.*

Upper tracing shows the G state of the aircraft. An episode of 1.8 G precedes 0 G, followed by another period of hypergravity. Some minutes of 1 G are flown before the next parabola. Lower traces show torsional positions of the two eyes. Left eye demonstrates offset after abrupt onset of 0 G.

parabola 6 of subject R.T., the torsional position of the eyes came together, and by parabola 9 (Fig. 2) the position of the eyes had reversed, with the right eye showing CCW torsion, which continued throughout the remainder of the flight. This positional reversal of eye offset was not observed in any other subject.

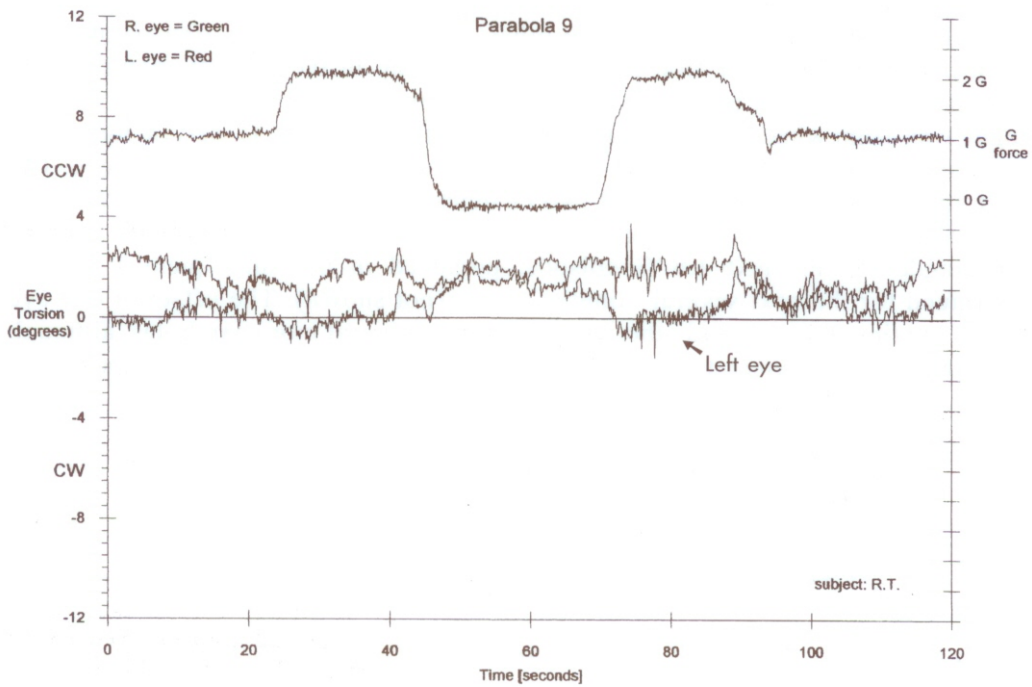

Fig. 2. - *Parabola 9 of subject R.T. shows the eyes have reversed the torsional positions seen in parabola 1 (Fig. 1).*

The right eye moves CCW, while the left eye hovers around the pre-parabola baseline. The left eye shows CCW response to 0 G but then reverts to baseline, unlike the first parabola where the left eye remains in an offset CCW position.

Offset can be more clearly appreciated when only the 1 G portions of the flight are shown. The mean eye torsion during 1 G between each parabola is plotted in Figure 3, illustrating subject P.V.'s response. His left eye began a CW rotation by parabola 2, increasing as the flight progressed. In contrast, the right eye had a tendency to cyclic CCW rotations.

Another subject, F.C., showed a similar but opposite pattern (Fig. 4), with the left eye torting CCW and the right CW, sometimes separating more than 8°. The offset of his eyes during the flight was marked and chaotic. In the three subjects shown above and in two others, it was apparent that the two eyes were behaving independently in all three gravitational states.

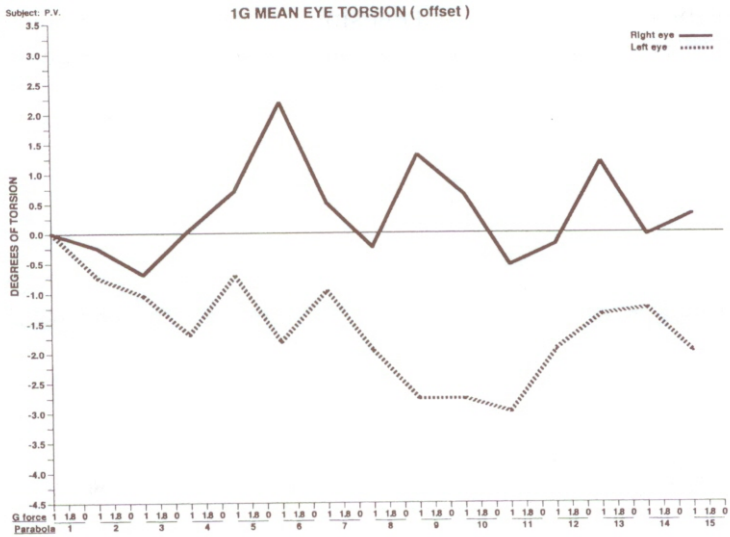

Fig. 3. - *Mean eye torsion in the 1 G portions of the flight between each parabola are shown for subject P.V.*

Both eyes show CW offset in parabolas 2 and 3. Subsequent parabolas have the left eye consistently CW, while the right eye begins a CCW offset, with cyclic returns to baseline. This independent behavior of the two eyes is noted in five of eight subjects.

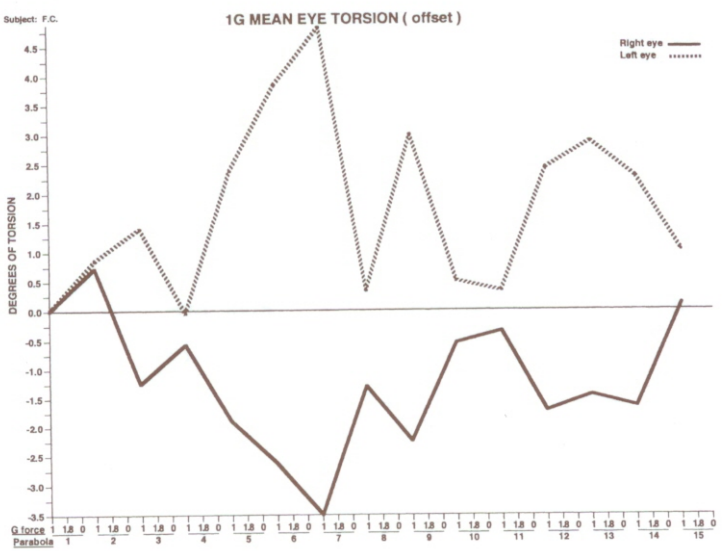

Fig. 4. - *A dramatic differential offset of the eyes is seen in subject F.C.*

His right eye is consistently torted CW compared to his pre-parabola baseline, while his left eye shows CCW rotation ranging from none in parabola 4 to 4.8° in parabola 7. His right eye in parabola 7 is torted CW -3.5°.

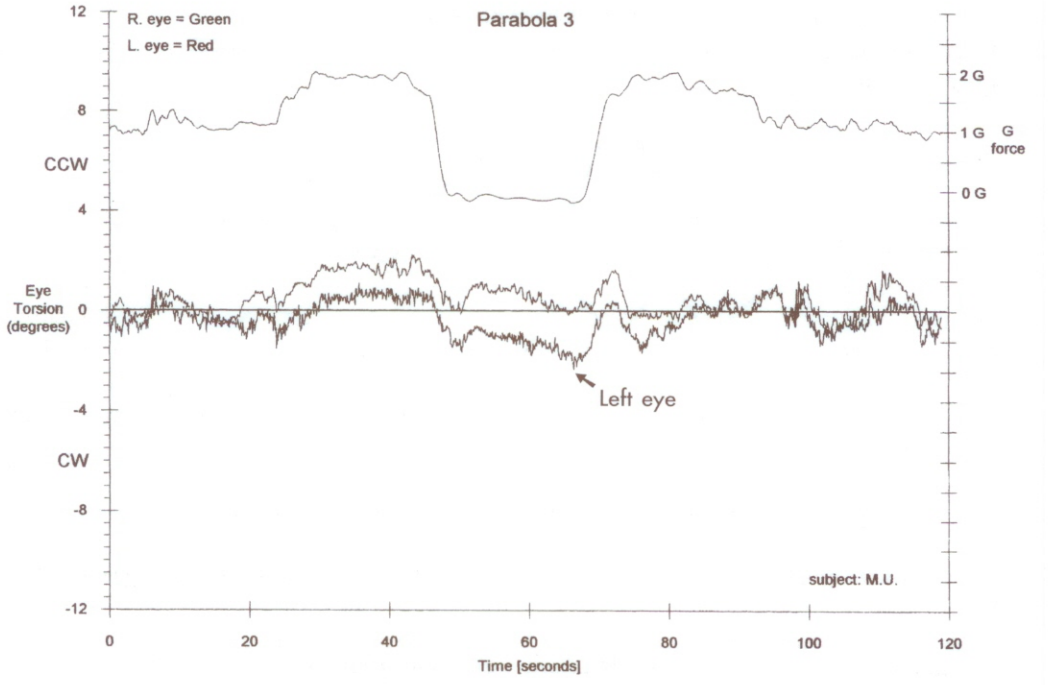

Fig. 5. - *Parabola 3 of subject M.U. shows the eyes responding to changes in G.*

At 1.8 G both eyes tort CCW and change torsional direction in response to 0 G. Subjects' heads were upright throughout the flight with gravity perpendicular to the major plane of the utricles and parallel to the saccules. The minimal responses seen are thought to result from hair cells on the curved utricular surfaces and not from the saccule (see text).

Table 1. - *Consistent torsional responses to novel gravitational states with head held motionless in upright position.*

	1.8 G				0 G			
	Right Eye		Left Eye		Right Eye		Left Eye	
	CW	CCW	CW	CCW	CW	CCW	CW	CCW
N.P.		+		+	+		+	
H.M.		+		+	+		+	
M.U.		+		+	+		+	
R.T.			+					+
L.P.								
P.V.			+					+
B.P.							+	
F.C.				+	+			

2. *Ocular torsion in response to novel G states.*

With subjects seated motionless in the upright position, torsional responses during the 1.8 G and 0 G states could be detected in most subjects. As noted above, G was directed along the subject's z axis. Figure 5 shows subject M.U. responding with CCW torsion in both eyes to 1.8 G, and with CW torsion in both eyes to 0 G.

Table 1 summarizes the consistent (i.e. at least 12 parabolas) changes in eye torsion of all 8 subjects. Although subjects N.P., H.M. and M.U. all had binocular CCW torsion in 1.8 G and binocular CW torsion in 0 G, subjects R.T. and P.V. showed the opposite pattern in only one eye with the other eye having no consistent pattern. The only consistent response in subject B.P. was CW torsion of the left eye in 0 G, while F.C. had CCW torsion of the left eye in 1.8 G and CW torsion of the right eye in 0 G. Only one subject, L.P., showed no consistent response in either eye to 1.8 G or 0 G.

3. *Disturbances of torsional conjugacy induced by 1.8 G and 0 G.*

To determine if the two eyes were moving conjugately moment to moment during the 1.8 and 1 G episodes, it was necessary to null the differential offset. This

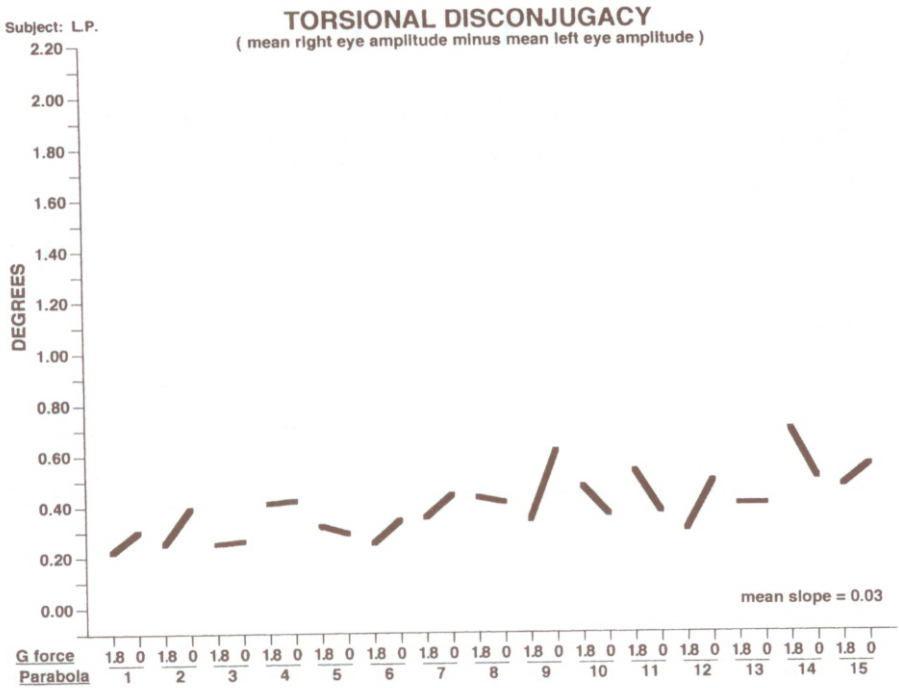

Fig. 6. - *Subject L.P. is an example of a low disconjugacy score.*

Distance from baseline shows the mean amplitude difference of the two eyes. The slope of the lines indicates the difference in response to the two novel G states. A series of shallow slopes with no consistent direction results in a low mean score of 0.03.

was achieved by using the mean offset portion of each eye in each parabolic segment to normalize the data in that segment, enabling a point-by-point calculation of the difference between the two eyes. These differences were then summed and a mean obtained, deriving a disconjugacy score for that segment without the confounding contribution of the offset. Using a method described elsewhere (9, 20) to demonstrate changes in disconjugacy in response to the novel G states, a mean slope provided a summary score indicating consistency and magnitude of the torsional disconjugacy over the course of all parabolas. Figure 6 shows subject L.P., who had small amounts of disconjugacy in both 1.8 G and 0 G. The mixture of positive and negative slopes indicates no consistent disconjugacy in either G state; the positive and negative values largely cancel one another, and the mean score is a low 0.03.

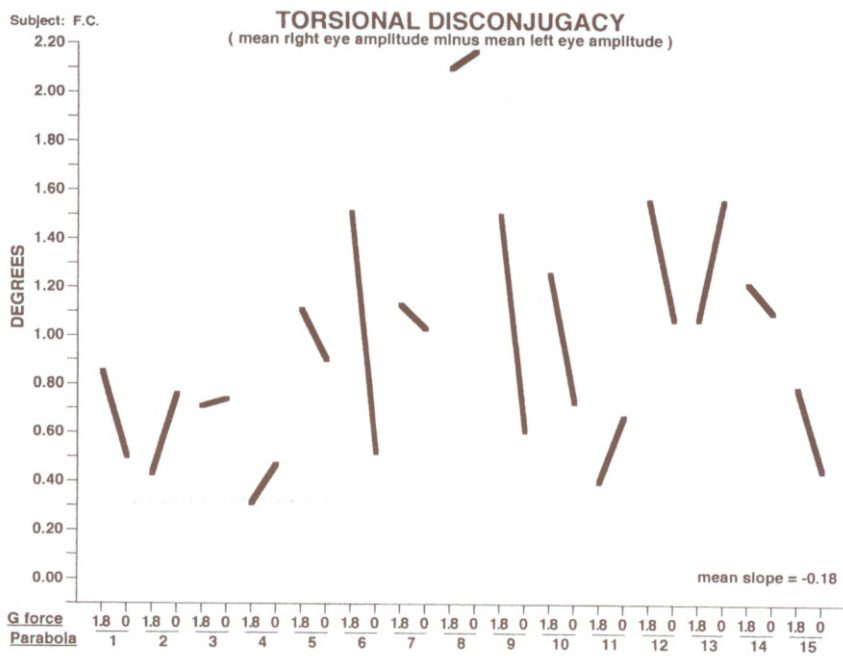

Fig. 7. - *In contrast to the subject in Figure 6, subject F.C. has a greater mean difference in torsional amplitude of the eyes and a greater difference in response to 1.8 G than to 0 G.*

The slopes are steeper and predominantly negative, and the combination results in a higher mean slope of -0.18.

Figure 7 illustrates greater disconjugacy in subject F.C., particularly in the 1.8 G segments. This results in steeper slopes, mostly negative in direction, with a score of -.18, a six-fold greater result than subject L.P. The other six subjects had disconjugacy scores ranging from 0.03 to .23. It should be noted that the magnitude of the score is important, but that the sign is irrelevant, simply denoting whether

the predominant slopes are positive or negative. Based on values obtained in previous studies (9, 20), the scores of .23 and -.18 lead us to predict these subjects would experience SMS; and the remainder would not. The two astronauts had scores of -.09 and .04 and did not experience SMS on their space missions.

When questioned, all subjects denied any visual disturbances during the flight.

DISCUSSION

This binocular study affirms that vestibular control of eye movements, particularly torsional eye movements, is not always conjugate. This is particularly true in novel hyper- or hypogravitational states. In normal individuals, at 1 G on Earth, torsional eye movements tend to be conjugate, particularly during slow dynamic changes as seen during naso-occipital and submental-vertex (barbecue) rotations (19). Spontaneous torsional eye movements are also largely conjugate as the subject sits quietly upright, with approximately ± .75° variation about the baseline (11). But in short-term hyper- and hypogravity, as seen during parabolic aircraft flight (27), and long-term hypogravity, as seen during spaceflight (10), disconjugate torsional eye movement results, sometimes of considerable magnitude.

Offset, one kind of disconjugacy, began in the sudden, usually abrupt transition of G state in the first parabola of parabolic flight (Fig. 1). This offset persisted during and between subsequent parabolas, often increasing in magnitude. One possible explanation might be displacement of the otoconia and/or physical deformation of their supporting membranes (16, 17, 28, 36). Alternatively, asymmetries in the oculomotor plant or orbital mechanics may be responsible. Could the torsional offset be non-vestibular in origin (15), possibly from abdominal gravitational receptors (25, 26)? There are too many unknowns to support this notion. Possibly a change in tonic firing rate of first order afferents may occur from an absence of customary stimulation of the otolith receptor cells. Bracchi et al. (2) found frog otolith afferents had marked changes of resting firing rate over several days in space.

Unfortunately, we cannot describe the time course of the recovery in the present parabolic flight experiment. The failure of the eyes to return to their baseline positions during the 1 G portions of flight suggests that readaptation to asymmetry, once the system is disrupted, is a process of some duration. This is supported by the finding that after spaceflight, similar torsional offset and disconjugacy remained abnormal at least through 13 days, having returned to normal when next examined months later (10).

In considering ocular torsion induced by 1.8 and 0 G states, the heads of our subjects were upright, the naso-occipital axes were in the long axis of the aircraft, and there was no independent head motion. The shallow bowl-like shape of the idealized human utricles are said to be oriented to each other at an angle of 210° to 214° open angle upward and 20° to 50° open angle forward to the Reid horizontal plane which passes through the inferior margins of the orbits and the centers of the external auditory canals (3, 5, 29). The major planes of the utricles

in this experiment were nearly perpendicular to the force of gravity, and the shearing effect of the otoconia on the underlying hair cells induced by the 1.8 and 0 G episodes was modest. Yet, Curthoys et al. (4) note both utricular and saccular maculae have such pronounced curvature that dorsoventral shear forces will stimulate regions of both organs. Neglecting this curvature and noting the substantial response to z-axis linear acceleration can lead to the conclusion that the saccule has about 25% impact on ocular torsion (6).

The saccules also have a shallow bowl-like shape, are positioned nearly vertical, and make an angle to the Reid plane of 90°-122° and 10°-33° with the median plane (3, 5). Thus, the shearing effect on saccule hair cells in 0 and 1.8 G with the head upright is substantial. If the saccules have a major projection to the oculomotor torters, one would expect significant and consistent ocular torsion across subjects. Such was not seen.

Let us now consider the relative contributions of the utricles and saccules to ocular torsion.

1. The elegant experiments of Uchino and colleagues in the cat show the utricles have strong multisynaptic projectors to the extraocular motoneurons, including the inferior oblique and trochlear motoneurons (34). On the other hand, saccular-activated vestibular nucleus neurons, which project preferentially to the spinal cord (32, 35), were only rarely (4 of 46) activated antidromically on stimulation of the oculomotor nuclei (32).

2. Stimulation of the cat utricular nerve as it exits from the inferior surface of the utricle, using 40-50 m bipolar steel electrodes causes non-conjugate, rotatory and slightly contralateral eye movements (21, 33).

On the other hand, when the saccule or saccular nerve in the cat is electrically stimulated, the eye movements are predominantly vertical. This suggests the otolith-ocular torsional reflex is predominantly of utricular origin.

3. When human subjects undergo horizontal sinusoidal linear acceleration along their y-axis, maximally stimulating the utricles, there is substantial ocular torsion (namely ± about 3°). When subjects were positioned so the stimulus was directed along their z-axis, maximally stimulating the saccules, the ocular torsion was modest (about ± 1°) [see Figure 1 in Merfeld et al. (24)]. This also suggests the predominant sense organ for ocular torsion is the utricle.

4. With the head in the upright erect position, as it is in the present experiment, the saccule is the otolith organ predominantly stimulated by vertical acceleration (12, 13, 14, 23). The directional reversals of ocular torsion as the aircraft changes from 0 G to 1.8 G are small, in some subjects of opposite polarity to other subjects, and in one subject are absent. This suggests that the saccules, which are substantially and uniformly stimulated across subjects are not the key sensory organs controlling ocular torsion; and the near-horizontally position utricles are.

5. Human ocular counterrolling during roll-tilt and centrifugation confirm that dorsoventral shear is important for determining ocular counterrolling. However, the relative contribution of utricles and saccules is not described (18).

6. Two patients, whose superior vestibular nerve was sectioned, showed the same abnormal responses in a test of dynamic ocular counterrolling as patients who

had had complete vestibular nerve sections (7). A similar finding was subsequently seen in a third patient. On the other hand, a patient with only the inferior vestibular nerve sectioned had a normal counterrolling response (unpublished data). These results also suggest the otolith-ocular torsion reflex is of utricular origin.

We conclude, particularly in the context of the present experiment, that the utricles are the main effector organs for the otolith-ocular torsion reflex, but the saccules may make a minor contribution.

The projections from the utricles to the eye muscle motoneurons are complex and multisynaptic. There may be at least partial independent projection to the two eyes. Several lines of evidence support this, all of them induced by novel G states.

1. The torsional eye movements in subject F.C., in which 1.8 G induced the left eye to tort CCW, and the eye to CW rotation in 0 G seem to indicate separate innervation to the two eyes. So do the torsional eye movements in only one eye in subjects R.T. and B.P.

2. Ocular torsion tends to be conjugate in normal subjects during dynamic testing in which subjects are slowly rotated to 90° right and left ear down (7). Yet, in cases with unilateral labyrinthectomy, the remaining utricle projects to both eyes–but in an asymmetrical and inconsistent fashion.

3. It has been shown that each vestibular nucleus has separate neuronal pathways to each eye (22, 37).

We conclude the present data supports at least partly independent projection of the utricle to the two eyes.

The sudden displacement of torsional eye position occurred abruptly in the first parabola, accompanying the first sudden G change. This may be due to displacement of otoconia on their underlying hair cells or other perturbation of otoconia-hair cell mechanics (16, 17, 28, 36). In spite of this, the subjects continued to show mild directional reversals of eye torsion with the 0 and 1.8 G states. Another explanation might be loss of compensation at a brainstem level in a system whose intrinsic asymmetry has adapted to a stable 1 G state.

In the past, we have demonstrated a relation between SMS and ocular disconjugacy of variable and increasing amplitudes during the course of increasing number of parabolas (9, 20). This earlier work was based on the means of three observations at each episode of 1.8 G and 0 G. In the present work, several hundred observations were made at each episode. Of the present eight subjects, we predict two subjects with scores of -.18 and .23 would be vulnerable to SMS, and the others would not. The two astronaut subjects had low scores and neither had SMS on their space missions, thus supporting our earlier results. The remaining subjects have not been in space.

SUMMARY

To examine otolith-governed ocular torsion in hyper- and hypogravity, eight subjects, including two astronauts, underwent parabolic flight while seated upright with head fixed. A mask fitted with two video cameras provided synchronized

images of both eyes at a rate of 25/sec during 15 parabolas, the individual parabolas separated by a few minutes of level 1 G flight. Three main findings emerged: 1) After the first parabola, most subjects showed differential torsional offset of the two eyes in the 1 G portions between parabolas, compared to the conjugate baseline position of the eyes prior to the first parabola. 2) Changes in binocular torsion in the 0 G and 1.8 G portions of parabolic flight revealed in most subjects systematic reversal of direction. The reversal was consistent within, but not across subjects. 3) Disconjugacy defined as the moment-to-moment difference in the movements of the two eyes, and evaluated without the contribution of the differential offset, found two subjects with relatively high disconjugacy scores, and the remaining six with low scores. On the basis of prior studies (9, 20), we would predict the first two would be subject to SMS, the remainder not. The two astronauts, who did not have SMS on their space missions, fell into the low scoring group.

We propose that the disconjugacies may be due to intrinsic asymmetries in the otolith receptors on the two sides of the head, which appear to be independently linked to the extraocular muscles of the two eyes, a phenomenon masked in normal 1 G states by adaptation. The apparently independent control of the two sides cannot be detected by the simpler and more common monocular studies.

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