NAMI-1080

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JOINT REPORT

NAVAL AEROSPACE MEDICAL INSTITUTE

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION

July 1969

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Bureau of Medicine and Surgery
MR005.01.01-0021

NASA Order R-93

Released by

Captain M. D. Courtney, MC USN
Commanding Officer

16 July 1969

*This study was conducted under the sponsorship of the Office of Advanced Research and Technology, National Aeronautics and Space Administration.

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SUMMARY PAGE

THE PROBLEM

The purpose of this experiment was to investigate the effect of varying the time interval between two equal and opposite Coriolis accelerations upon the duration of the subjective responses evoked by the second stimulus. It was also designed to evaluate certain predictions generated from a "torsion pendulum" model of the neural events mediating these subjective phenomena.

FINDINGS

Theoretical curves derived from the torsion pendulum model approximated fairly closely the way in which the reported durations of the subjective phenomena increased as a function of the time interval between the two Coriolis accelerations. This result supported the a priori assumption that the neural events underlying the subjective phenomena are closely linked to mechanical events occurring within the cupula-endolymph system. However, an explanation resting entirely upon peripheral phenomena would be inadequate to account for two additional findings: 1) The estimated time constants of signal decay were shorter than those expected on the basis of the known mechanics of the semicircular canal system, and 2) the persistence of the Coriolis sensation (feelings of apparent whole body motion without visual reference) was greater at all intervals than the Coriolis oculogyral illusion (OGI). Adequate explanation of these findings requires the postulation of additional central mechanisms.

A secondary finding was that subjective reactions to the stimulus producing a pitch-forward sensation or a downward displacement of the OGI target were consistently more persistent than those produced by the equal but opposite stimulus. This result was compatible with findings of earlier studies.

ACKNOWLEDGMENTS

We gratefully acknowledge the advice given to us by Dr. Alan Benson of the Royal Air Force Institute of Aviation Medicine, Farnborough, England. In addition, we should like to record our indebtedness to Mr. Roy Garlock who assisted in the collection of data.

INTRODUCTION

This investigation was concerned with the situation in which a Coriolis accelerative stimulus (S_1) is followed after a different time interval (I) by a second stimulus (S_2) that is equal in magnitude but opposite in direction to the first. The Coriolis stimulation was delivered to the semicircular canal system by a 45° head tilt to the left shoulder (S_1) followed, after the variable interval, by a return motion to the upright position (S_2) during rotation at constant velocity. The effect of varying the time interval (I) was studied in relation to two measures of subjective response: 1) the duration of the sensation of pitching about the body's y-axis (termed the "Coriolis sensation"), and 2) the duration of the apparent motion of a dimly illuminated target (termed "the Coriolis oculogyral illusion" or OGI).

A "torsion pendulum" model (see Figure 1) was used to generate the experimental predictions. The basic assumption of the model was that the neural events underlying the perception of the subjective phenomena would be dependent upon the physical events occurring within the vestibular end-organ. This formulation allowed the known mechanical properties of the cupula-endolymph system (4,12) to be used as the basis for predictions concerning the duration of the subjective phenomena evoked by S_2.

The uppermost plot in Figure 1 indicates the initial magnitude and time-course of the neural signal evoked by the first Coriolis acceleration, S_1. This neural activity is assumed to decay exponentially with a time-constant of $\frac{1}{k}$ and has the form: $y_1 = Ae^{-kt'}$ (where: y_1 = magnitude of the neural signal evoked by S_1; t' = time from onset of S_1). After 1 second, an equal yet directionally opposed stimulus, S_2, is delivered to the cupula-endolymph system which causes the signal to reverse its sign in the manner shown in Figure 1. The initial extent of this signal reversal due to S_2 is assumed to be equal to the peak signal value, A, evoked by S_1. The peak magnitude of the signal produced by S_2 is designated B where: $B = -A-Ae^{-kt'}$. This signal also decays exponentially with a time-constant of $\frac{1}{k}$. Hence, the neural response to S_2 is of the form: $y_2 = [A\ (1 - e^{-kI})]e^{-kt}$ (where: y_2 = magnitude of the neural response evoked by S_2; t = time after S_2). It is also postulated that the subjective phenomena mediated by y_2 will cease when $y_2 = C$, a threshold value. Thus, the persistence of the subjective phenomena evoked by S_2 is expected to increase as a function of I up to a certain asymptotic value as shown in the following equation:

$$T_{R_2} = \frac{1}{k} \log_e \left(\frac{1 - e^{-kI}}{D}\right)$$

where
T_{R_2} = duration of the subjective response evoked by S_2 (seconds)
$\frac{1}{k}$ = time-constant of signal decay (seconds)
D = C/A or the ratio of peak to threshold signal
I = interval between S_1 and S_2 (seconds)

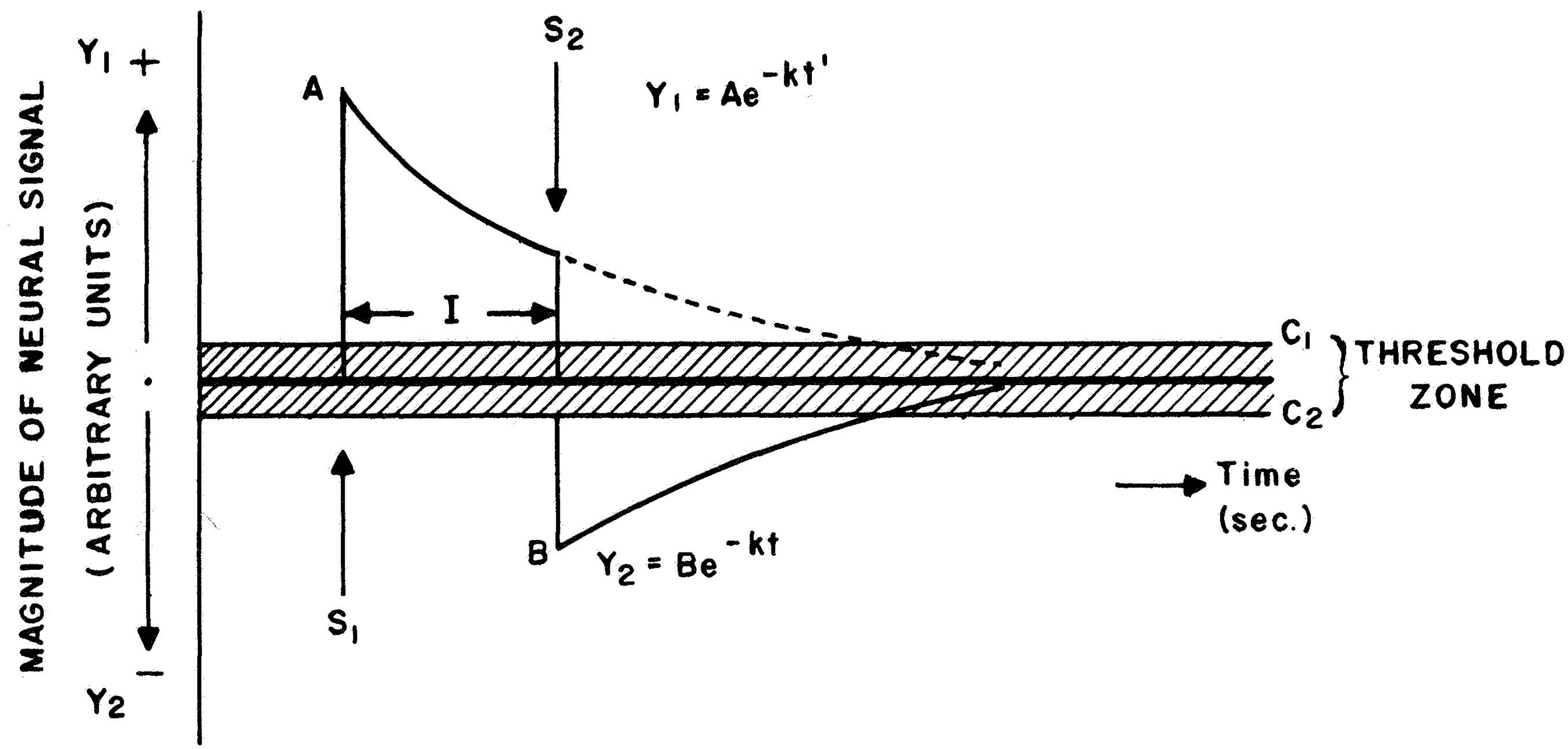

Figure 1

Diagrammatic representation of the "torsion pendulum" model.
(See text.)

PROCEDURE

SUBJECTS

Twenty young men, either Navy enlisted men or college students, served as subjects. All were known to possess normal vestibular function and to be in good health at the time of the experiment.

METHOD

The experiment was performed in the Pensacola Slow Rotation Room (SRR). A full description of this facility can be found elsewhere (3).

The subjects were seated with their backs to the inside wall of the SRR at a distance of 7 feet from the center of rotation. The subjects' z-axes were aligned parallel to the axis of rotation. Head pads attached to the wall restricted the lateral head movements to a tilt through an arc of 45° to the left shoulder and back to the upright. The head movements were made at a uniformly rapid rate and were completed within 0.25 second. The rotation was in the counterclockwise (CCW) direction throughout.

In thirteen subjects, the effects of the Coriolis accelerations were measured by recording the persistence of the OGI. The OGI target consisted of a dimly illuminated 6-inch cube placed at a distance of 10 feet from the subject. Only the outline of the cube was illuminated, and it was oriented such that eight edges were visible to the subject. For these measurements, the SRR was in complete darkness except for the target and a small light attached to the experimenter's clipboard. The latter was screened from the subject by a curtain.

In the other seven subjects, the effects of the same accelerations were measured by recording the persistence of the Coriolis sensation, i.e., the time elapsing between the completion of the head movement and the point at which the subject reported no further sensation of apparent bodily motion. For these measurement, the subjects were blindfolded throughout the session.

The stimulus procedures were identical for both the OGI and sensation groups. Rotation started at 7.5 rpm. At this speed, each subject began by executing three sets of controlled tilt and return movements, where the interval between any two motions was kept fixed at 30 seconds. On completion of each discrete movement, the subject indicated the persistence of his apparent visual or bodily motion. This procedure (termed "fixed-interval motions") was included to provide a baseline persistence value for the subjective response to S_2 when the interstimulus interval was such that the response to S_1 would have largely dissipated before S_2 was applied. It also provided the subjects with an opportunity to stabilize their endpoint decision criteria prior to the variable-interval determinations.

Some 5 minutes after the completion of the fixed-interval measurements, the variable-interval motions were commenced. The intervals (I) between S_1 (tilt) and S_2 (return) were: 1, 2, 4, 8, 16, and 32 seconds. The movements were made on verbal instructions from the experimenter, and only the response to S_2 was recorded. The intervals were presented in a random order, and a different random sequence was used for each subject.

On completing these measurements at 7.5 rpm, the subjects were rested for approximately 5 minutes with head immobilized. The angular velocity of the SRR was then increased to 10 rpm where fixed and variable-interval movements, identical to those described above, were executed.

One departure from this procedure was the fact that the 32-second interval was not included into the design until five of the OGI subjects had been tested. Thus, while persistence values for this interval were obtained for all seven of the "sensation" subjects, they were obtained for only eight of the OGI subjects.

RESULTS

The mean persistence values evoked by S_1 and S_2 during the initial fixed-interval movements at 7.5 and 10 rpm are shown in Tables I (a) and I (b). Table I (a) shows the duration values for the OGI subjects, while Table I (b) shows the durations for the sensation subjects. Grand means and standard deviations are given at the bottom of each table.

Inspection of these tables indicates that S_2 evoked a more persistent response, both for OGI and sensation subjects, than the tilt motion S_1. The Wilcoxon matched-pairs signed ranks test (10) showed that these differences were significant for all comparisons: OGI at 7.5 rpm ($T = 6.5$; $p < .01$, 2-tailed test); OGI at 10 rpm ($T = 2.0$; $p < .01$, 2-tailed test); Coriolis sensation at 7.5 rpm ($T - 0$; $p < .05$, 2-tailed test); Coriolis sensation at 10 rpm ($T - 0$; $p < .02$, 2-tailed test).

The findings from the variable-interval measurements at 7.5 and 10 rpm are shown in Tables II (a) and II (b); the former shows the results for the OGI subjects, while the latter gives those for the sensation subjects. Since the mean persistence values for both OGI and sensation subjects were not significantly different at 7.5 and 10 rpm, the values obtained at these velocities were averaged to give a typical OGI and a typical sensation response at each $S_1 - S_2$ interval. These averaged values are shown graphically in Figure 2. Also shown on this graph are the baseline persistence values for S_2 obtained from the fixed-interval measurements. It can be seen that these baseline values correspond very closely to the asymptotic values obtained in the variable-interval measurements.

Figure 2 shows that the persistence curves for the OGI and sensation subjects are of the same form; the major point of difference is that the averaged OGI values are some 40 per cent less than the corresponding sensation values at each time interval. The similarity of these two curves is brought out more clearly by the graph shown in

Table I (a)

Mean Persistence of the OGI Following Three Sets of Fixed-Interval (30 sec) 45° Tilt and Return Motions

	Counterclockwise Rotation 7.5 rpm		10 rpm	
Subject	Tilt (S_1)	Return (S_2)	Tilt (S_1)	Return (S_2)
1	3.2	3.5	2.2	2.3
2	3.0	3.7	2.3	4.8
3	10.0	11.0	7.8	9.5
4	1.0	1.2	1.0	1.3
5	5.2	8.5	3.5	8.0
6	4.2	5.0	3.3	3.8
7	1.8	2.0	1.5	1.3
8	4.5	4.3	4.5	6.0
9	0	5.3	0	8.0
10	2.3	4.7	2.0	5.5
11	1.3	1.0	1.3	2.2
12	0.8	1.0	0	1.2
13	2.0	5.0	2.0	6.2
$\overline{X}$:	3.02	4.32	2.41	4.62
SD:	2.60	2.92	2.07	2.85

Table I (b)

Mean Persistence of the Coriolis Sensation Following Three Sets of Fixed-Interval (30 sec) 45° Tilt and Return Motions

	Counterclockwise Rotation 7.5 rpm		10 rpm	
Subject	Tilt (S_1)	Return (S_2)	Tilt (S_1)	Return (S_2)
1	6.8	10.7	9.0	11.2
2	4.0	4.0	2.7	3.8
3	6.3	6.5	7.7	9.2
4	7.3	7.8	7.0	7.5
5	5.3	8.7	4.5	9.0
6	3.7	5.0	3.5	6.0
7	7.7	14.2	8.5	13.3
$\overline{X}$:	5.87	8.12	6.13	8.57
SD:	1.58	3.49	2.53	3.17

Table II (a)

Mean Duration of Coriolis Sensation Evoked by S_2 as a Function of Interval $S_1 - S_2$ (N = 13)

OGI Values						
Interval (sec):	1	2	4	8	16	32
7.5 rpm	0.4	1.8	2.7	3.3	4.1	4.3*
10 rpm	1.0	1.4	2.9	4.0	4.7	5.1*
Grand mean+	0.67	1.58	2.81	3.63	4.38	4.62
SD	1.16	1.76	2.55	2.55	2.94	2.95

* = N = 8

+ = Average of 7.5 and 10 rpm values

Table II (b)

Mean Duration of Coriolis Sensation Evoked by S_2 as a Function of Interval $S_1 - S_2$ (N = 7)

Coriolis Sensation Values						
Interval (sec):	1	2	4	8	16	32
7.5 rpm	2.0	2.0	4.0	5.8	8.2	8.3
10 rpm	1.3	2.5	4.6	6.1	7.5	7.9
Grand mean	1.68	2.32	4.32	6.00	7.86	8.14
SD	1.42	2.04	2.44	2.62	3.40	3.51

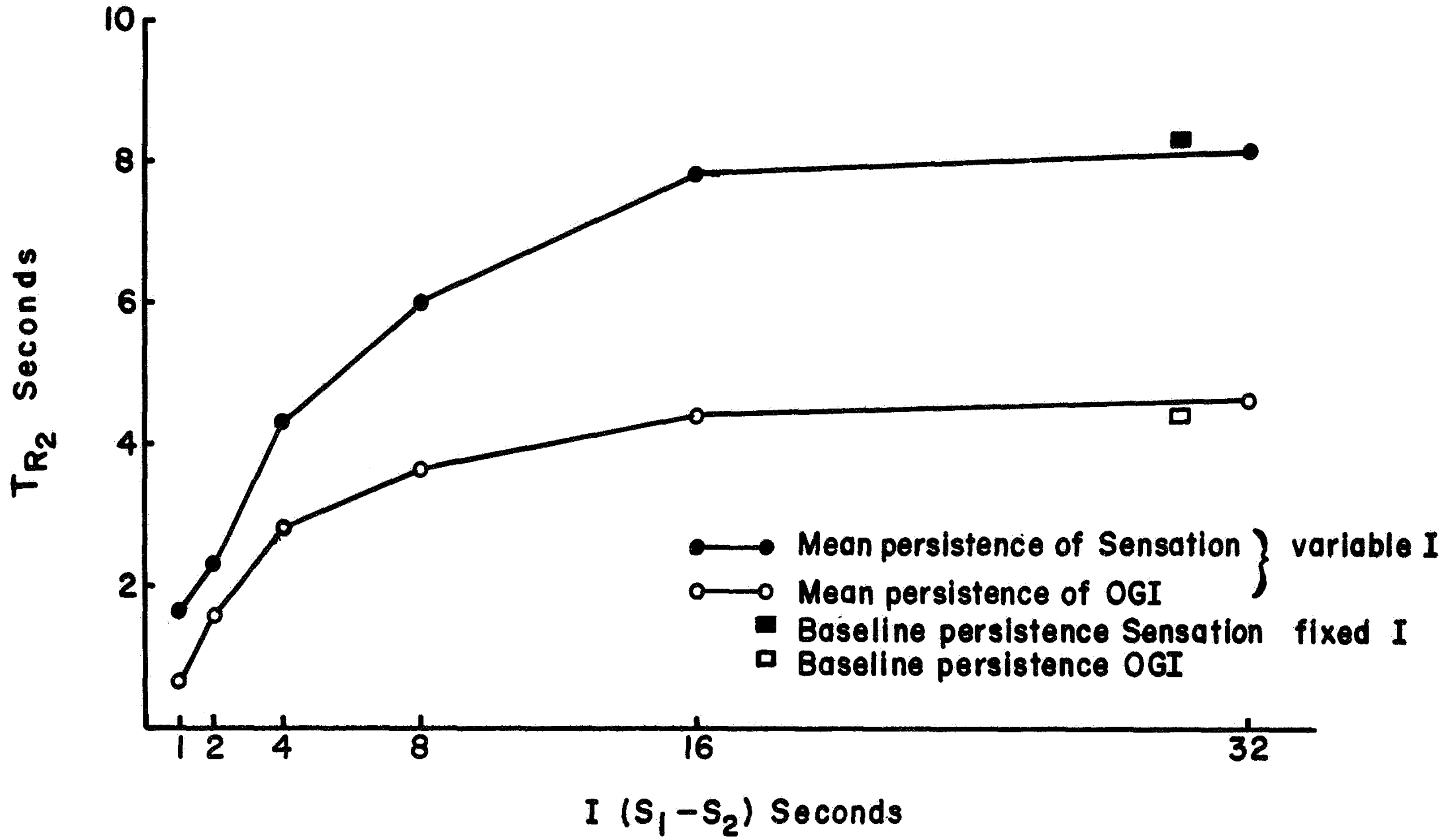

Figure 2

Mean persistence (T_{R_2}) of the Coriolis sensation and the oculogyral illusion (OGI) due to the second stimulus (S_2) as a function of the time interval (I) between the first and second stimuli ($S_1 - S_2$). Also shown are the average sensation and OGI persistence values obtained from the fixed interval measurements. Both sets of data represent the average of the 7.5 and 10 rpm conditions.

Figure 3 in which each mean value for sensation and OGI has been multiplied by a factor chosen to normalize their respective asymptotic values to 10 seconds. In the case of the OGI group, this factor was 2.13, whereas for the sensation group, it was 1.25.

The next consideration was how well these observed OGI and sensation persistence values corresponded to the theoretical expectations of the torsion pendulum model. Figure 4 shows an attempt to fit the observed persistence values for the OGI and sensation by theoretical curves derived from the predictive equation. This was achieved by manipulating the two unknowns, D and k, until an optimum fit was found for each set of obtained values. For the sensation plot, the theoretical curve was fitted with $D = 0.192$ and $k = 0.212$ where $1/k = 4.72$ seconds; in the case of the OGI values, the theoretical curve was fitted with $D = 0.257$ and $k = 0.298$ where $1/k = 3.36$ seconds. It can be seen that while the theoretical points at the x-intercept and the asymptote approximated the observed values, those in the midrange of I intervals tended to overestimate the observed points for both the sensation and the OGI curves.

DISCUSSION

Although incidental to the main purpose of this experiment, it is interesting to note that the subjective responses to the return motion (S_2) were significantly longer than those for the preceding tilt motion (S_1) during the initial fixed-interval measurements. During CCW rotation, the tilt motion produces a sensation of pitching backwards or an upward movement of the OGI target, while the return motion has the opposite effects. Guedry and Montague (6) in their investigation of the psychophysics of the Coriolis reactions noted a similar disparity in the subjective magnitude of certain responses associated with pitch-down and pitch-up sensations elicited by the same type of stimulus. In a more recent study, the present authors (9) also found that magnitude estimates of pitch-down sensations were consistently greater than those for pitch-up sensations produced by Coriolis stimuli of comparable magnitude.

Inasmuch as the theoretical curves (see Figure 4) derived from the torsion pendulum model approximate fairly closely the obtained OGI and sensation persistence values, the present findings appear to support the a priori assumption that the neural events underlying the perception of these subjective phenomena are closely related to the mechanical events occurring within the cupula-endolymph system. However, an entirely peripheral explanation would be inadequate to account for: 1) the finding that the estimated time-constants of signal decay (4.72 seconds for sensation, and 3.36 seconds for OGI) were considerably shorter than those expected on the basis of theoretical equations governing the mechanics of the canal system (12); and 2) the finding that the persistence of the Coriolis sensation was proportionately longer than that for the OGI at each time interval.

Theoretical analyses of the Coriolis vestibular reaction (6,8) have shown that the net effect of the type of stimulus used in this experiment is equivalent to that of a simple impulsive stimulus with the head fixed relative to the axis of rotation. With a

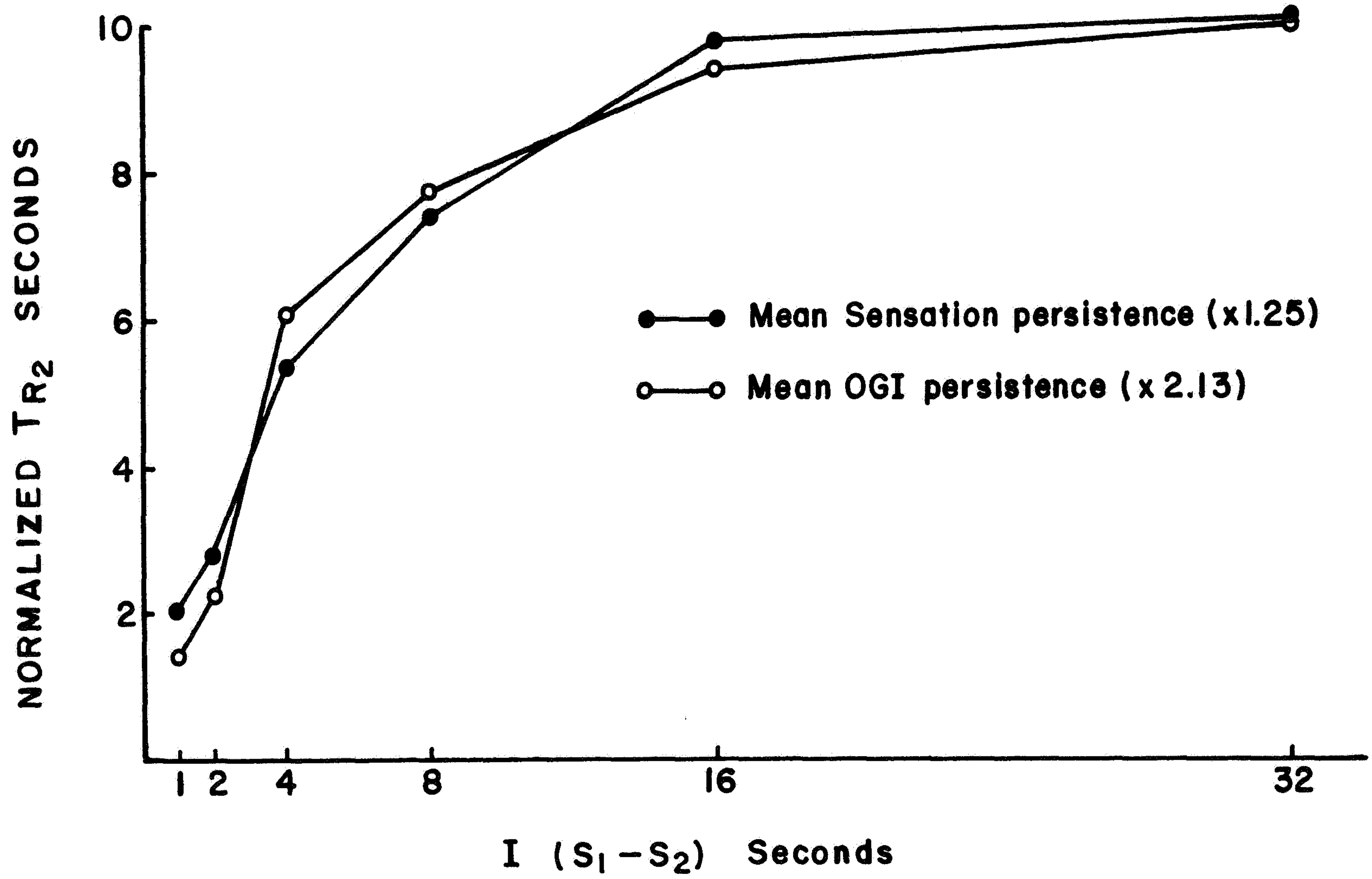

Figure 3

Normalized Coriolis sensation and oculogyral illusion (OGI) persistence curves. Each mean duration for sensation and OGI has been multiplied by a factor chosen to normalize the asymptotic values to 10 seconds.

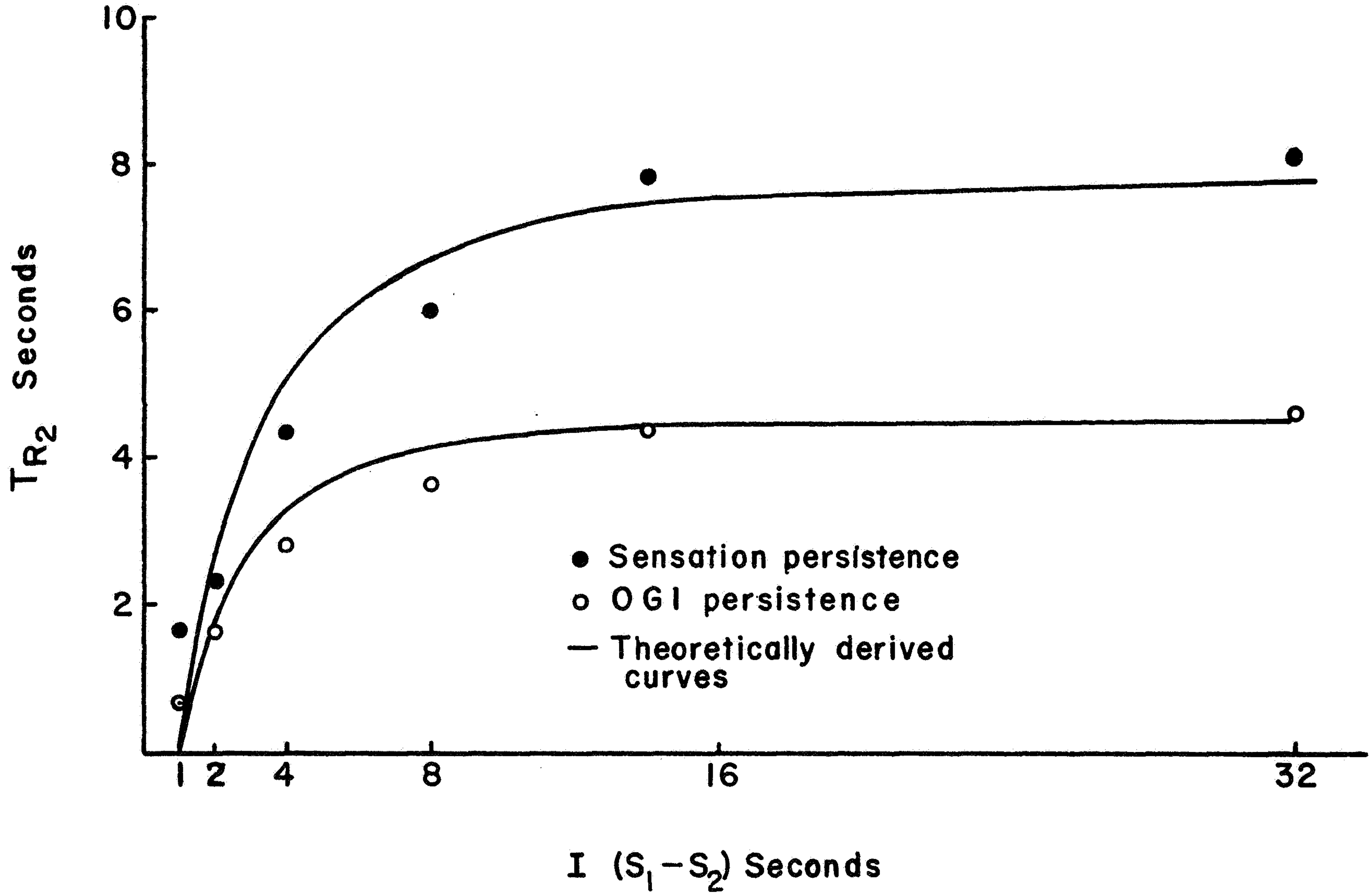

Figure 4

Comparing observed Coriolis sensation and oculogyral illusion durations with those predicted from the theoretical equation. (See text.)

45° head movement, however, the magnitude of the cupula deflection will be somewhat less than that produced by a simple angular impulse at corresponding angular velocities. Although there is some relative reduction in response magnitude, it is insufficient to account for the greatly reduced time-constants obtained in this and similar investigations involving Coriolis stimulation (6,7). The rate at which the cupula deflection is annulled by its intrinsic restoring couple should remain constant irrespective of the magnitude of the initial deflection.

A more probable explanation of this phenomenon is one which postulates some intervention by central mechanisms. Both during and immediately after the "Coriolis evoking" head motion, the sensory inputs from the canals and otoliths are in conflict, whereas in the case of the simple impulsive stimulus, the two inputs are normally synergistic. This suggests that the canal signal is suppressed when contradictory gravireceptor information is present at the same time. This hypothesis receives additional support from the findings of experiments involving rotation around an Earth-horizontal axis (2,5) and those involving the repositioning of the subject following rotation around the vertical axis (1). In both cases, the nystagmus and sensation time-constants were considerably shorter than those obtained from simple impulsive stimuli of equivalent magnitude.

The proportionately greater persistence of the Coriolis sensation poses a more difficult problem of explanation since the results from conventional cupulometric studies tend to indicate the contrary finding. Van Dishoeck et al. (11), using averaged cupulograms, showed that the OGI is consistently more persistent than the sensation of rotation over the same range of impulse values.

The values of D and k used to generate the best-fitting theoretical curves (see Figure 4) suggest that the time-constant of the signal mediating the OGI was somewhat shorter and the threshold level higher than that for sensation. Since both phenomena stem initially from the same end-organ activity, it is unlikely that these values reflect the mechanical events within the cupula-endolymph system; more probably, they reflect differences in the transducing properties of the central pathways mediating the two subjective responses.

An additional factor, and one which may also explain the contradictory findings with respect to cupulometry, is that the OGI target used in the present experiment was a relatively large 6-inch cube, whereas in most of the cupulometric studies the target has been a much smaller source of light. It seems reasonable to suppose that a relatively large target having a clearly definable geometric form is more resistant to apparent motion than a smaller, less-defined target. Thus the inherent "stability" of the present OGI target is likely to manifest itself in a reduced duration of sensation.

Finally, it is worth noting that these findings suggest a technique for minimizing the undesirable consequences of Coriolis stimulation during the early preadapted stages of exposure to a rotating environment. To obtain the greatest advantage from the "damped swing door" characteristics of the cupula-endolymph system, a necessary head motion should be followed as rapidly as possible by an equal and opposite movement. The present results show that even if this complementary motion is delayed for as long as 4 seconds, there is about a 40 per cent loss of sensation persistence with respect to the maximum. For intervals of less than 4 seconds, the persistence curve drops precipitately so that at 2 seconds there is approximately a 75 per cent loss, and at 1 second the reduction is in the region of 80 to 100 per cent of the maximum value. It seems reasonable to assume that these persistence losses would also reflect corresponding reductions in the initial magnitude of the subjective phenomena.

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Unclassified
Security Classification

DOCUMENT CONTROL DATA - R & D

(Security classification of title, body of abstract and indexing annotation must be entered when the overall report is classified)

1. ORIGINATING ACTIVITY (Corporate author)	2a. REPORT SECURITY CLASSIFICATION
Naval Aerospace Medical Institute Pensacola, Florida 32512	Unclassified
	2b. GROUP N/A

3. REPORT TITLE
THE EFFECT OF VARYING THE TIME INTERVAL BETWEEN EQUAL AND OPPOSITE CORIOLIS ACCELERATIONS

4. DESCRIPTIVE NOTES *(Type of report and inclusive dates)*

5. AUTHOR(S) *(First name, middle initial, last name)*

James T. Reason and Ashton Graybiel

6. REPORT DATE	7a. TOTAL NO. OF PAGES	7b. NO. OF REFS
16 July 1969	14	12

8a. CONTRACT OR GRANT NO.	9a. ORIGINATOR'S REPORT NUMBER(S)
NASA Order R-93	NAMI-1080
b. PROJECT NO. BuMed MR005.01.01-0021	
c.	9b. OTHER REPORT NO(S) *(Any other numbers that may be assigned this report)*
d.	163

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11. SUPPLEMENTARY NOTES	12. SPONSORING MILITARY ACTIVITY

13. ABSTRACT

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Unclassified
Security Classification

KEY WORDS	LINK A		LINK B		LINK C	
	ROLE	WT	ROLE	WT	ROLE	WT
Coriolis vestibular reaction						
Oculogyral illusion						
Semicircular canal mechanics						