

ADAPTATION TO VESTIBULAR DISORIENTATION

VI. Eye-Movement and Subjective Turning Responses to Varied Durations of Angular Acceleration

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I. Introduction

Ocular nystagmic responses elicited by angular acceleration have been found to be different in cat and in man.⁶ With prolonged stimuli (36 sec), a rise and decline of nystagmus during stimulation was obtained from cats for both lateral- and vertical-canal stimulation. Human subjects did not exhibit a comparable decline during prolonged stimulation. Nystagmic reactions of the cat thus resembled the subjective (rather than the nystagmic) reactions of human subjects.^{9,10,12,19,20}

At least part of the difference noted above in regard to primary nystagmic reactions appears related to the prominent secondary nystagmus which characterizes responses of the cat to angular accelerations. Secondary nystagmus is opposite in direction to the primary response, and it may reflect a process which develops during, and opposes continuation of, the primary reaction.

The present investigation represents an extension of the earlier study.⁶ A range of stimulus durations was used to clarify relations between stimulus duration, the rate of decline of primary nystagmus, and the intensity of secondary nystagmus, and to compare further vestibular processes in cat and man.

II. Methodology

A. Cats

Apparatus. Rotational stimulation was provided in a light-proof room with the Huffman Rotation Device.⁷ Angular accelerations and decelerations were $4^\circ/\text{sec}^2$ separated by 54 sec of constant velocity. Animals were tested in pairs (with their heads at the center of rotation) by means of a set of tiers.⁸

Restraint. Restraint was effected by the method of Henriksson, Fernandez, and Kohut¹⁵ and in the manner described elsewhere.⁶

Recording. An Offner Type R Dynograph recorded horizontal components of eye movements from needle electrodes inserted by the outer canthi. A 3-sec time constant was used in amplification.

B. Human Subjects

Apparatus. A Stille-Werner RS-3 rotator was programmed to provide accelerations and decelerations of $4^\circ/\text{sec}^2$ separated by 2 min of constant velocity.

Recording. An Offner Type T polygraph (time constant: 3 sec) recorded horizontal components of eye movements from surface electrodes taped by the outer canthi.

III. Procedure

Each of 12 cats and 12 human subjects received 6 rotatory trials comprising $4^\circ/\text{sec}^2$ accelerations and decelerations for 1.2, 3, 9, 15, 21, and 30 sec. Rotation was always counterclockwise and the order of presentation of the stimulus durations was counterbalanced among pairs of subjects as indicated in Table 1.

TABLE 1. Order of presentation of stimulus durations (in seconds). Durations varied from 1.2 to 30 sec. All angular accelerations were $4^\circ/\text{sec}^2$ and rotation was always counterclockwise. Only the lateral canals were stimulated.

Human Subjects	Cats	Trials					
		1	2	3	4	5	6
Pz & Ch	108 & 109	1.2	3.0	9.0	15.0	21.0	30.0
Dy & Do	110 & 111	3.0	9.0	15.0	21.0	30.0	1.2
Sa & Br	112 & 113	9.0	15.0	21.0	30.0	1.2	3.0
Dt & Da	114 & 115	15.0	21.0	30.0	1.2	3.0	9.0
Te & Ro	116 & 117	21.0	30.0	1.2	3.0	9.0	15.0
Ve & Pa	118 & 119	30.0	1.2	3.0	9.0	15.0	21.0

None of the subjects had been used in previous vestibular experiments. Human subjects (6 men and 6 women) were instructed to signal onset and cessation of their rotatory experiences by means of a signal key.

Scoring. Slow-phase displacement of the eyes was scored by measuring the peak to base-line distance for each beat of nystagmus and summing these values for 3-sec intervals. Time measurements were also made from the end of each stimulus (a) to the end of the primary response and (b) to the start of the secondary nystagmus. The number of beats of primary nystagmus which followed stimulus termination was tabulated.

IV. Results and Discussion

A. Cats

Measures of both response time and the number of beats of primary nystagmus following stimulus termination appear in Table 2. Post-stimulus responses of greatest duration and magnitude occurred when stimulus durations were between 3 and 15 sec with the maximum post-stimulus primary response occurring, in general, with stimuli of 9 sec duration.

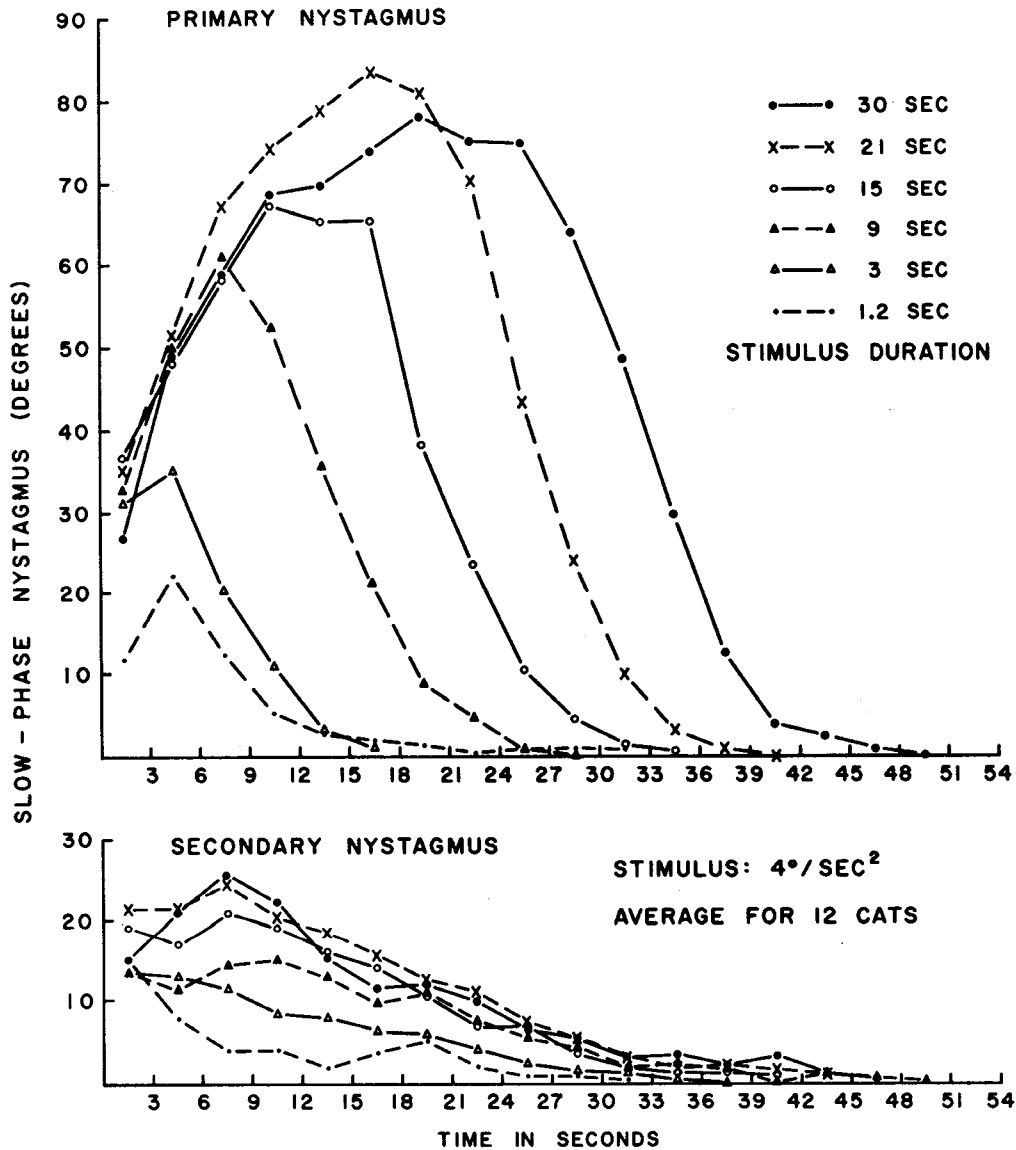


FIGURE 1. Time-course plots of slow-phase eye displacement per 3-sec interval for 12 cats exposed to 6 stimulus durations of $4^{\circ}/\text{sec}^2$ angular accelerations. For the 21 and 30 sec durations, responses reach a peak and begin to decline during the stimulus. For the two shortest durations, the peak response occurs after stimulus termination. Peak magnitude of the secondary reactions appears related to stimulus duration.

TABLE 2. Measures of primary nystagmus following the termination of each rotatory stimulus for cats. Each response value is a mean of responses to an acceleration and a deceleration stimulus. Stimuli were 4°/sec² for 1.2, 3, 9, 15, 21, or 30 seconds.

Cat	Time From End of Stimulus to End of Primary Nystagmus (Sec)					
	1.2	3.0	9.0	15.0	21.0	30.0
108	10.9	12.4	14.6	10.6	8.1	6.0
109	5.9	8.3	8.2	5.4	4.0	1.6
110	18.5	7.3	9.2	12.0	5.0	2.3
111	7.1	11.1	8.8	6.5	4.3	7.2
112	3.0	12.4	11.6	15.7	12.2	10.8
113	2.8	11.8	9.8	9.4	6.0	3.8
114	8.2	11.6	9.3	8.0	13.6	6.8
115	10.2	8.0	10.2	10.6	13.1	9.0
116	11.5	12.1	14.2	15.3	12.4	11.3
117	7.6	3.0	8.2	9.3	6.2	5.0
118	8.9	12.3	13.3	13.3	12.5	12.1
119	10.4	10.7	7.2	5.0	7.2	2.5
M=	8.8	10.1	10.4	10.1	8.7	6.5

	Time From End of Stimulus to Start of Secondary Nystagmus (Sec)					
	108	15.6	15.4	20.8	15.6	14.5
109	7.9	16.9	13.5	9.9	6.5	6.2
110	15.9	6.6	12.9	6.0	8.4	6.7
111	15.0	16.8	12.6	10.8	7.5	10.6
112	—	14.6	17.5	24.4	20.4	18.1
113	15.7	18.3	14.1	11.6	9.0	7.5
114	12.5	12.7	14.7	25.4	15.4	15.6
115	17.3	19.5	14.6	16.7	15.0	14.0
116	13.6	16.9	21.3	17.5	15.4	16.1
117	11.2	18.0	14.8	12.6	13.0	15.6
118	9.3	16.3	15.3	15.5	16.4	15.7
119	15.2	14.9	11.8	11.4	9.5	7.1
M=	13.6	15.6	15.3	14.8	12.6	12.2

	Beats of Primary Nystagmus After End of Stimulus					
	108	2.0	12.0	19.0	12.5	11.5
109	1.5	7.0	9.0	6.5	2.5	1.0
110	3.0	3.0	6.5	6.5	4.0	3.0
111	2.5	7.0	8.5	7.0	4.0	2.0
112	2.5	8.0	14.0	18.5	16.5	9.5
113	2.0	7.5	9.5	9.0	5.0	3.0
114	5.5	8.5	12.0	7.5	17.0	5.5
115	4.5	7.0	8.5	9.5	16.5	10.5
116	5.5	8.0	16.0	18.0	9.5	18.5
117	4.0	5.0	—	8.5	5.0	12.0
118	12.0	15.5	17.0	19.5	19.0	15.0
119	4.0	8.0	5.5	4.5	7.0	1.5
M=	4.1	8.0	11.4	10.6	9.8	7.3

TABLE 3. Measures of primary nystagmus following the termination of each rotatory stimulus for human subjects. Each response value is a mean of responses to an acceleration and a deceleration stimulus. Stimuli were 4°/sec² for 1.2, 3, 9, 15, 21, or 30 seconds.

Subject	Time From End of Stimulus to End of Primary Nystagmus (Sec)					
	1.2	3.0	9.0	15.0	21.0	30.0
Pa	22.0	11.0	17.3	32.0	16.8	22.3
Da	12.6	25.2	42.4	54.1	64.6	45.3
Br	—	28.8	20.5	25.7	37.5	29.6
Do	18.3	19.6	38.9	51.3	36.3	39.8
Ch	13.1	25.1	40.0	33.0	24.5	23.9
Ro	13.6	41.3	28.4	34.9	44.2	40.5
Ve	10.9	62.2	44.0	41.3	38.4	37.9
Te	—	20.9	42.6	26.7	33.1	27.2
Dt	31.8	42.0	44.4	48.4	40.1	35.7
Sa	21.3	22.3	55.6	44.1	32.8	28.8
Pz	7.3	29.1	57.9	40.3	39.2	28.5
Dy	17.6	46.3	42.4	45.6	33.7	29.2
M=	16.9	31.2	39.5	39.8	36.8	32.4

	Time From End of Stimulus to Start of Secondary Nystagmus (Sec)					
	Pa	—	—	—	—	—
Da	—	—	—	—	—	67.3
Br	—	—	—	—	—	—
Do	—	—	—	—	—	—
Ch	—	—	30.6	42.8	28.3	27.1
Ro	—	—	72.7	41.3	51.4	45.4
Ve	—	—	48.8	46.1	40.2	38.1
Te	—	11.4	23.0	17.1	34.1	35.9
Dt	31.8	40.2	44.4	58.8	40.1	35.7
Sa	21.3	—	—	32.2	32.9	28.8
Pz	—	—	57.7	41.9	39.2	35.3
Dy	—	—	50.4	50.0	33.7	31.9
M=	*	*	46.8	41.3	37.5	37.2

	Beats of Primary Nystagmus After End of Stimulus					
	Pa	13.0	13.0	19.5	36.5	39.0
Da	10.0	25.0	66.5	82.5	94.0	81.0
Br	—	27.0	11.5	29.0	33.0	29.5
Do	9.0	13.0	39.5	47.0	42.5	39.0
Ch	7.5	29.5	47.0	45.5	42.5	37.0
Ro	8.5	24.5	43.0	50.5	70.0	62.5
Ve	4.5	30.0	41.0	44.0	37.0	32.5
Te	—	23.0	53.0	46.0	51.5	38.5
Dt	12.0	39.5	55.5	63.5	59.5	55.5
Sa	20.0	31.5	78.5	73.0	52.5	54.0
Pz	4.0	12.0	34.5	34.0	28.5	24.0
Dy	15.0	20.5	47.0	51.0	46.5	43.5
M=	10.4	24.0	44.7	50.2	49.7	43.7

*Too few scores on which to base a mean.

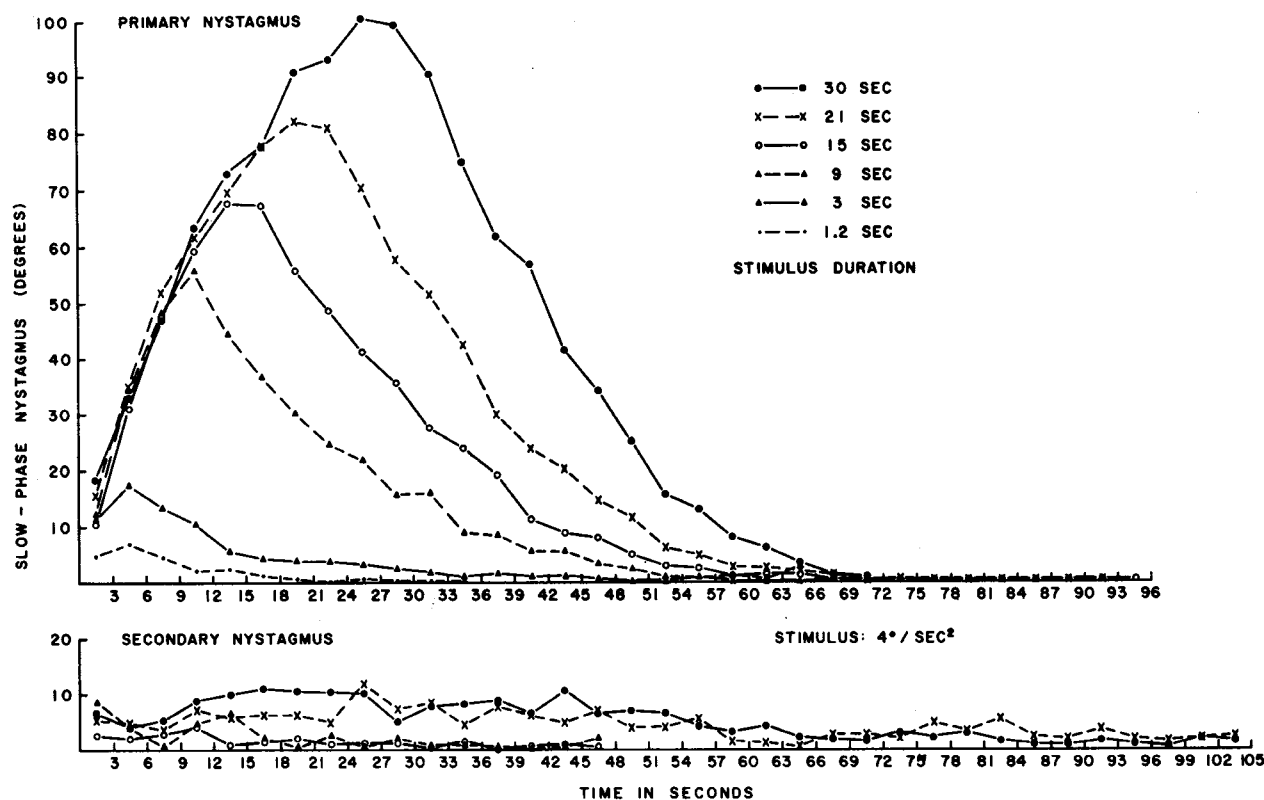


FIGURE 2. Time-course plots of slow-phase displacement per 3-sec interval for 12 human subjects exposed to 6 stimulus durations of $4^\circ/\text{sec}^2$ angular accelerations. No decline of nystagmus during stimulation is evident for any duration (compare with Figure 1). Note that the peak response for the three shortest durations occurs after stimulus termination. No secondary responses were evident for the 1.2 and 3 sec stimuli and not all subjects showed secondary nystagmus for the longer stimuli.

The slow-phase velocity of primary and secondary nystagmic responses was plotted for each of the 6 stimulus durations (Figure 1). For the 21 and 30 sec stimuli, there was a slight decline in response during constant angular acceleration. Consistent with data from cats in the earlier experiment,⁶ it appears that the nystagmic response reaches maximum intensity between 15 and 20 sec and declines after this, even though the stimulus is of constant magnitude and direction.

The peak magnitude of secondary nystagmus appears directly related to the duration of the angular acceleration. Secondary responses were obtained from all but one cat for the 6 stimulus-duration conditions; the exception (cat 112) gave no secondary nystagmus following the 1.2 second stimulus.

B. Human Subjects

Figure 2 shows little or no decline in human nystagmus during constant angular acceleration

irrespective of stimulus duration. This is consistent with human results of earlier studies,^{5,6,14} but it is in contrast with results from cats in which nystagmus declined after about 20 sec of constant angular acceleration.

With brief stimuli (1.2 sec and 3 sec), it appears that in both man and cat the slow-phase velocity of nystagmus continues to increase ("overshoots") after the stimulus terminates (Figures 1 and 2), whereas, with prolonged stimuli, slow-phase velocity of nystagmus declines immediately after (in humans) or before (in cats) the stimulus terminates (Figure 1).

As stimulus duration is increased up to about 15 seconds, the duration of the post-stimulus primary nystagmus increases. With longer stimuli, the duration of the post-stimulus primary response declines. In this respect human primary nystagmus corresponds fairly well in its temporal characteristics with the human subjective response. This is shown in Figure 3

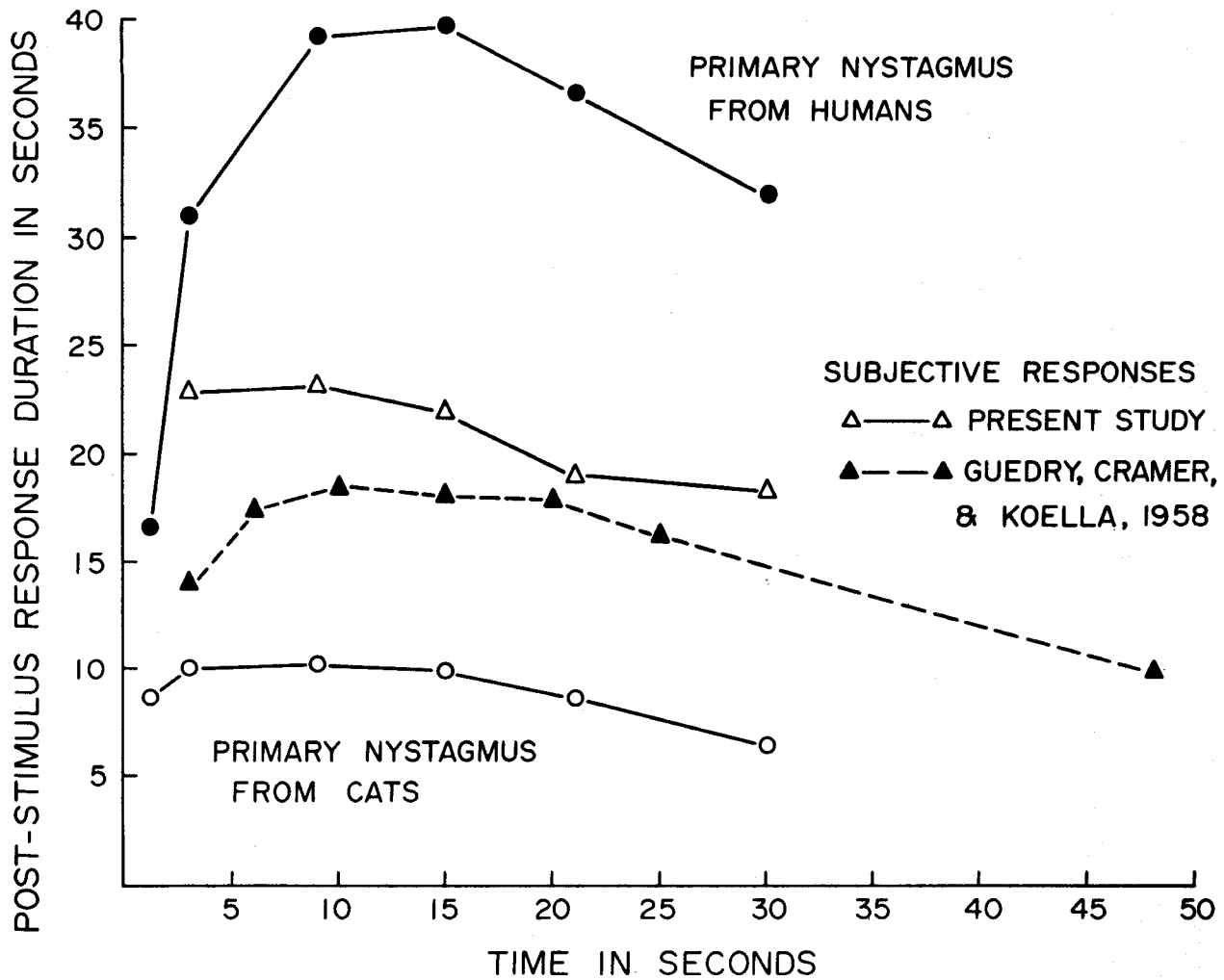


FIGURE 3. Duration of the post-stimulus subjective and nystagmic reactions obtained in this study are compared with subjective data from an earlier study. The abscissa represents stimulus duration. Functions depicted for the two sets of subjective data and for primary (slow-phase displacement) nystagmus from cats are in close agreement.

where the mean subjective turning scores from the present study are presented along with subjective data obtained in a previous study. In this earlier study,¹³ subjects had been trained in making subjective reports, whereas the present subjects had no preliminary practice. The rise and decline in duration of human nystagmus and subjective response as stimulus duration increases is also matched fairly well by the change in temporal characteristics of nystagmus in the cat, also shown in Figure 3. Reference to Tables 2 and 3 shows that, in both man and cat, time elapsed from stimulus termination to onset of secondary nystagmus increases and declines in a manner which approximately parallels duration of the primary reaction.

Secondary nystagmus was not evident in the recordings of any of the human subjects for the 1.2 and 3 sec stimuli, and several subjects gave no secondary response to the 30 sec stimulus. However, frequency of occurrence of secondary nystagmus increased with stimulus duration, and this may be interpreted as evidence for a relationship between stimulus duration and intensity of secondary response in humans similar to, but more variable than, that observed in the cat. In comparison with secondary nystagmus of the cat, the secondary nystagmus in man has a later onset, lower average intensity (relative to man's primary reaction), and seems to be more subject to individual differences.

Tables 2 and 3 suggest that the number of

beats of secondary nystagmus is more closely related to the duration of primary post-stimulus nystagmus than to the duration of the stimulus. This is in contrast to the maximum slow-phase velocity of secondary nystagmus which seems related to the stimulus duration, at least in the cat (see Figure 1). The decline in number of secondary beats with stimuli longer than 15 sec may signify an encroachment of the secondary reaction on the primary reaction.

Primary nystagmus in the cat is shorter in duration and has a lower beat-frequency than that of man for the range of stimuli investigated. There is also a pronounced difference between man and cat in regard to the intensity-ratio of secondary to primary nystagmus, the ratio being higher for the cat.

A log plot of nystagmus slow-phase velocity with respect to time also shows the cat to have

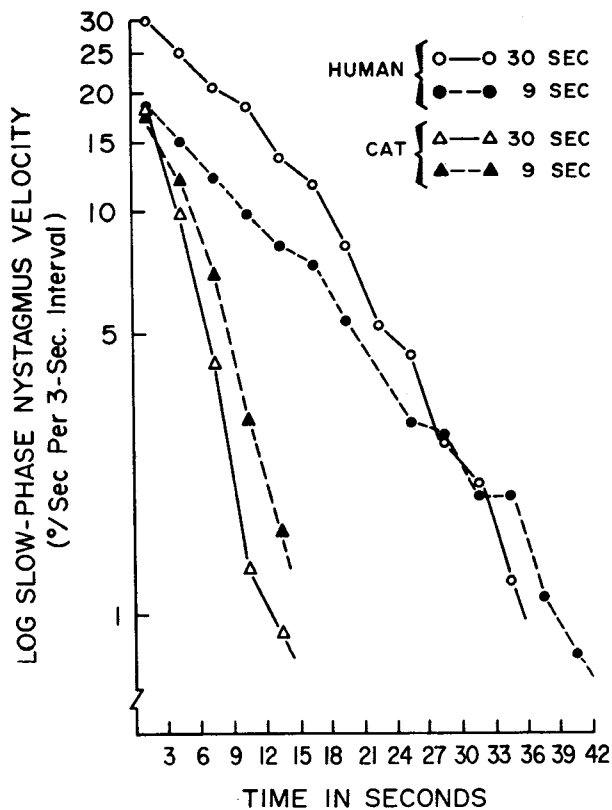


FIGURE 4. Log plots of slow-phase eye velocity following two stimulated durations for cat and human subjects. Data represent nystagmus measured from the point of stimulus termination and thus depict the rates of response decay. Decay is more rapid in cats and the longer stimulus duration produces more rapid declines.

a substantially different rate of decline of nystagmus (lower time constant) than man for comparable stimuli (see Figure 4). It also appears that the slope of nystagmus decline for both man and cat changes as a function of stimulus duration, the longer stimuli producing post-stimulus nystagmus with a higher rate of decay (lower time constant).

V. General Discussion

Because neurophysiological data from cats are sometimes applied to the explanation of reactions in man, it is important to compare the same response variables in men and cats exposed to identical vestibular stimuli. Nystagmus in cats declined during prolonged constant angular acceleration in spite of efforts to maintain alertness, whereas nystagmus in alert men did not decline during prolonged angular acceleration; the rate of decline of primary vestibular nystagmus following each stimulus was greater in cats than in man; the ratio of secondary to primary nystagmus was higher in cat than in man.

If it is assumed that secondary nystagmus reflects a process which develops during the primary reaction and opposes its continuation, then all of the differences between man and cat may be due to this secondary process in cat having a more direct control of nystagmus than does its counterpart in man. The characteristics of subjective data reported by man resembled the alterations of nystagmus in cats during and after prolonged angular accelerations,⁶ and in some respects the nystagmus of man deviates from both the nystagmus of cat and the subjective responses of man during and after these unusual stimuli. It appears that the hypothesized secondary process exerts a control on man's sensory experience, i.e., the perceived angular velocity, comparable to the control of nystagmus in the cat. This is not to say that the nystagmus of man is completely without the modulating influence of this secondary process because the rate of decline of both post-stimulus primary nystagmus and the occurrence of secondary nystagmus were influenced in man by the duration of the stimulus. However, the control is apparently less consistent and, hence, probably less direct for the range of stimuli used in the present experiment. (Subsequent experiments have illustrated a pronounced secondary nystagmus in

man when prolonged high-magnitude angular accelerations are used.)

It is parsimonious and reasonable to assume that a single process accounts for (a) the decline in response during prolonged angular acceleration, (b) the increased response decline following prolonged acceleration, and (c) the increased secondary response following prolonged acceleration. The possibility that the cupula endolymph system is under-critically damped, contrary to the common supposition, would explain a secondary response, but this seems at variance with much of the evidence for the over-damped Torsion Pendulum analogy of van Egmond, Groen, and Jongkees²¹ and could not explain findings (a) and (b). To explain these results on the basis of cupula deflection, it would be necessary to assume that the stiffness of the cupula increases during prolonged constant angular acceleration. Van Egmond, et al²¹ have proposed that events within the endorgan (either bioelectric, biochemical or plastic changes within the cupula) could account for secondary responses, and this possibility cannot be ruled out. Lowenstein¹⁶ has reported that increasing cupula deflection in elasmobranch initiates neural activity "in one after the other previously silent units" which often adapt themselves rapidly. Adrian² and recently Melvill Jones,¹⁷ recording from the vestibular nuclei in cats, found little evidence for rapid adaptation. However, Cappel⁹ has noted that slow declines in some units recorded in the vestibular nuclei of cats correspond temporally to declines in human subjective data. The possibility that there is a diminished sensory inflow during prolonged cupula deflection in cats remains open.

In man, one aspect of the vestibular reaction (subjective velocity) declines while another aspect (nystagmus) does not decline during prolonged acceleration.¹⁴ From this, it does not seem reasonable to attribute the decline of the one response to a suppression of sensory inflow. (Some reservations are necessary in this interpretation because average curves of different groups of subjects form the basis of the conclusion. Subjective and nystagmic data from the same subjects should be compared and studied for the presence of correlation.) Aschan and Bergstedt² have evidence which implicates the central nervous system in secondary responses. Prolonged primary responses induced by uni-

lateral caloric stimulation should provide an opportunity for adaptive changes within the cupula; yet Aschan and Bergstedt² reported little or no secondary nystagmus with unilateral caloric stimuli, whereas bilateral hot/cold caloric stimuli and rotational stimuli, yielding primary responses of equivalent length, produced secondary responses.

Although secondary nystagmus (and apparently associated response modulation) in man and cat are probably attributable to the central nervous system, it remains quite possible that some of the differences between man and cat are attributable to differences in the properties of endorgans; e.g., the shorter primary nystagmic response in cats (irrespective of stimulus duration) is probably attributable to a greater cupula spring-action in cat. Response parameters of the central nervous system may be conditioned or inherently matched to the response parameters of the cupula-endolymph system so that the shaping of responses to unusual stimuli may be similar in form but on a different time base in different animals.

The conditions under which the "secondary processes" have been demonstrated, viz., prolonged constant angular acceleration, are seldom, if ever, encountered in natural movement. Even a single, brief, unidirectional angular acceleration followed by constant velocity does not occur in natural movement and, as noted in the present study, intensity of nystagmus continues to increase briefly beyond the termination of short unidirectional stimuli. In natural movement, any brief angular acceleration is immediately followed by angular acceleration of opposite sign which returns the cupula toward its position of static equilibrium. Hence, in the case of either brief unidirectional stimuli or prolonged unidirectional stimuli, the vestibular reactions fail to follow the theoretical¹¹ cupula deflection. However, this does not necessarily signify either an inadequate response system within the range of natural movements or a gross error in theoretical cupula mechanics. The departure from expected results signifies a range of unnatural stimuli which is not accurately followed due to either inaccurate sensory detection or unfaithful central following of the input, or both. Because the natural periods of movements of various animals are different,¹⁸ it is quite possible that the ranges of accurate sensory

representation of movement, due to central and peripheral differences, will differ slightly in different animals.

The functional significance of the secondary process is not established. Some pathological conditions undoubtedly yield a central imbalance of spontaneous input from the two ears, and the "secondary process" may serve to readjust the point of homeostatic balance. Some complex motions of the head and body may terminate with minor residual cupula deflections, and this could require minor shifts in the point of balance between the two ears, which would be accomplished too slowly by the elasticity of the cupula. Tolerance to an increased level of vestibular stimulation encountered in land, sea, and air travel may require a suppression at some level of vestibular inflow, and it is possible that this secondary process serves this function. It has been shown that standard test stimuli administered after an angular acceleration are influenced in proportion to the duration of the preceding angular acceleration,¹³ and it may be assumed that this finding is another manifestation of the "*secondary process*." Moreover, with repetitive angular accelerations, the peaks of both primary and secondary nystagmus in cats

diminish and shift toward earlier occurrences.^{4,6} This suggests that the secondary process encroaches more and more upon the primary reaction and thus limits the magnitude and duration of the primary reaction with repetitive stimulation. In humans, there are large individual differences in secondary nystagmus. If the secondary reaction is a manifestation of an adaptive process which serves to limit the primary reaction, it may prove to be an indicator, among people with comparable histories of motion exposure, of individual differences in ability to habituate to repetitive vestibular stimulation.

VI. Summary

A direct relationship between duration of acceleration and (a) decline of response during acceleration, (b) rate of decline of response after acceleration, and (c) magnitude of secondary reaction, is regarded as an indication of a central process which limits a prolonged vestibular primary reaction. The process is manifested by its influence on relatively basic reflex reactions (nystagmus) in the cat, and is more prominently manifested in man by its influence on sensory perception.

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