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SUMMARY PAGE

THE PROBLEM

Neurophysiological responses of cats are frequently studied in an attempt to understand perceptual and physiological responses of men. The purpose of the present experiments is to compare nystagmus responses of man and cat to equivalent vestibular stimuli to provide a basis for comparative interpretation of data.

FINDINGS

Nystagmus in alert cats declined during prolonged constant angular acceleration, whereas nystagmus in alert men did not decline under similar conditions. The rate of decline of primary nystagmus after application of each stimulus was greater in cats than in man. The ratio of secondary to primary nystagmus was higher in cat than in man. All of these effects may be manifestations of a central process which tends to suppress prolonged primary vestibular reactions. In cats this process influences nystagmic reactions which may be closely connected to sensory perceptions. In man, this process is evident by its influence on sensory perception and is not clearly manifest in nystagmic reactions of alert men.

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INTRODUCTION

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

At least part of the difference noted above in regard to primary nystagmus appears to be 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 among 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.

PROCEDURE

CATS

Apparatus

Rotational stimulation was provided in a lightproof room with the Huffman Rotation Device (7). Angular accelerations and decelerations were 4 deg/sec^2 separated by 54 seconds of constant velocity. Animals were tested in pairs (with their heads at the center of rotation) by means of a set of tiered boxes (8).

Restraint

Restraint was effected by the method of Henriksson, Fernández, and Kohut (15) 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 three-second time constant was used in amplification.

HUMAN SUBJECTS

Apparatus

A Stille-Werner RS-3 rotator was programmed to provide accelerations and decelerations of 4 deg/sec^2 separated by two minutes of constant velocity.

Recording

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

METHOD

Each of twelve cats and twelve human subjects received six rotatory trials comprising 4-deg/sec^2 accelerations and decelerations for 1.2, 3, 9, 15, 21, and 30 seconds. Rotation was always counterclockwise, and the order of presentation of the stimulus durations was counterbalanced among pairs of subjects as indicated in Table I.

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

Table I

Order of Presentation of Stimulus Durations (in Seconds)

Human Subjects	Cats	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

Scoring

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

RESULTS AND DISCUSSION

CATS

Measures of response time and of the number of beats of primary nystagmus following stimulus termination appear in Table II. Poststimulus responses of greatest duration and magnitude occurred when stimulus durations were between three and fifteen seconds, with the maximum poststimulus primary response occurring, in general, with stimuli of nine seconds' duration.

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

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

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 twenty seconds of constant angular acceleration.

With brief stimuli (1.2 and 3 seconds) 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 fifteen seconds, the duration of the poststimulus primary nystagmus increases. With longer stimuli the duration of the poststimulus primary response declines. In this respect human primary nystagmus corresponds

Table II

Cats: Measures of Primary Nystagmus Following Termination of Each Stimulus*

	Time from End of Stimulus to End of Primary Nystagmus (sec)					
Cat	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	13.2
109	7.9	16.9	13.5	9.9	6.5	6.2
110	16.9	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	6.5
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

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*Each response value is a mean of responses to an acceleration and a deceleration stimulus of 4 deg/sec^2 for indicated durations.

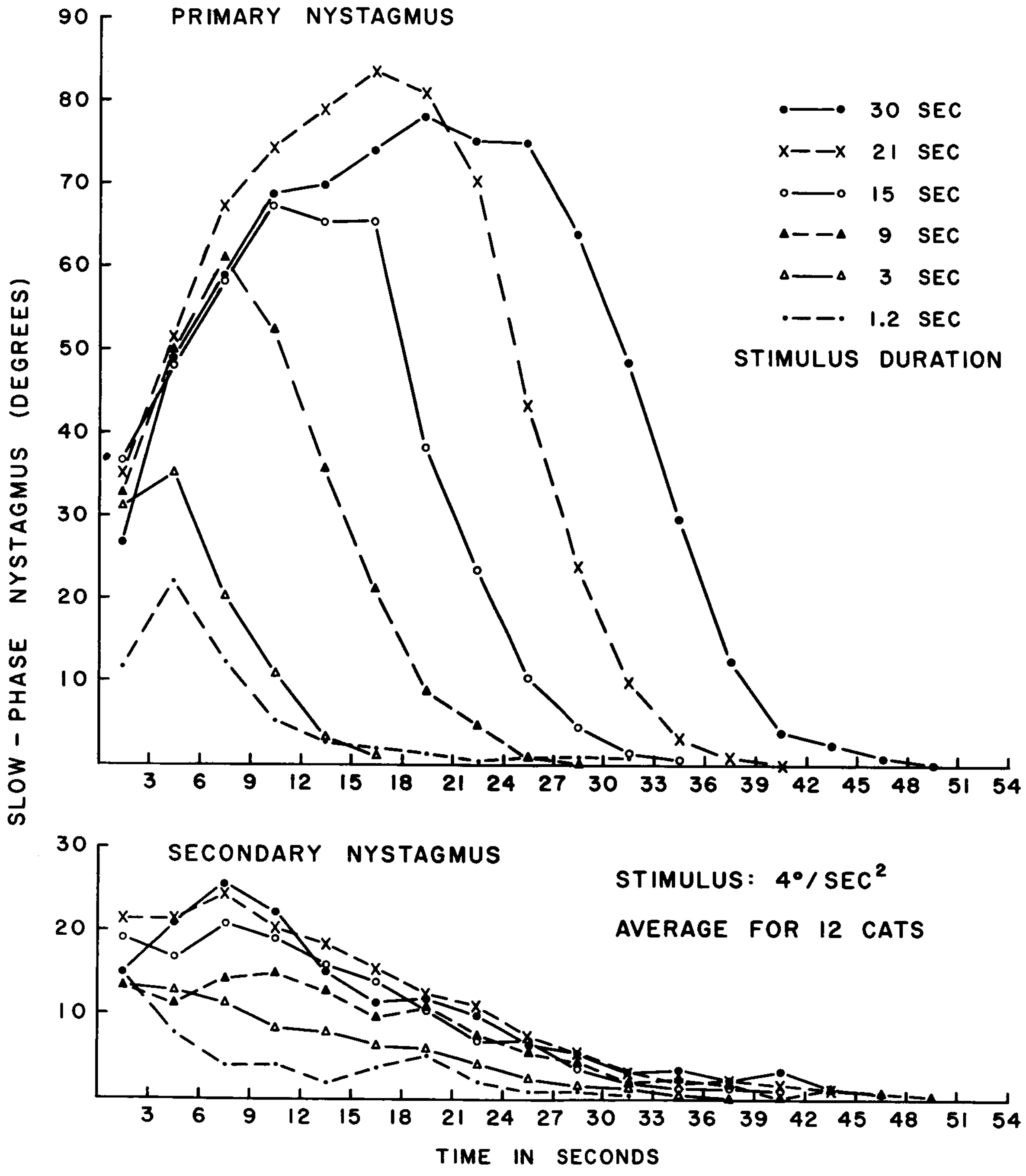

Figure 1

Time-Course Plots of Slow-Phase Eye Displacement per 3-sec Interval for 12 Cats Exposed to Six Stimulus Durations of 4°/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 to be related to stimulus duration.

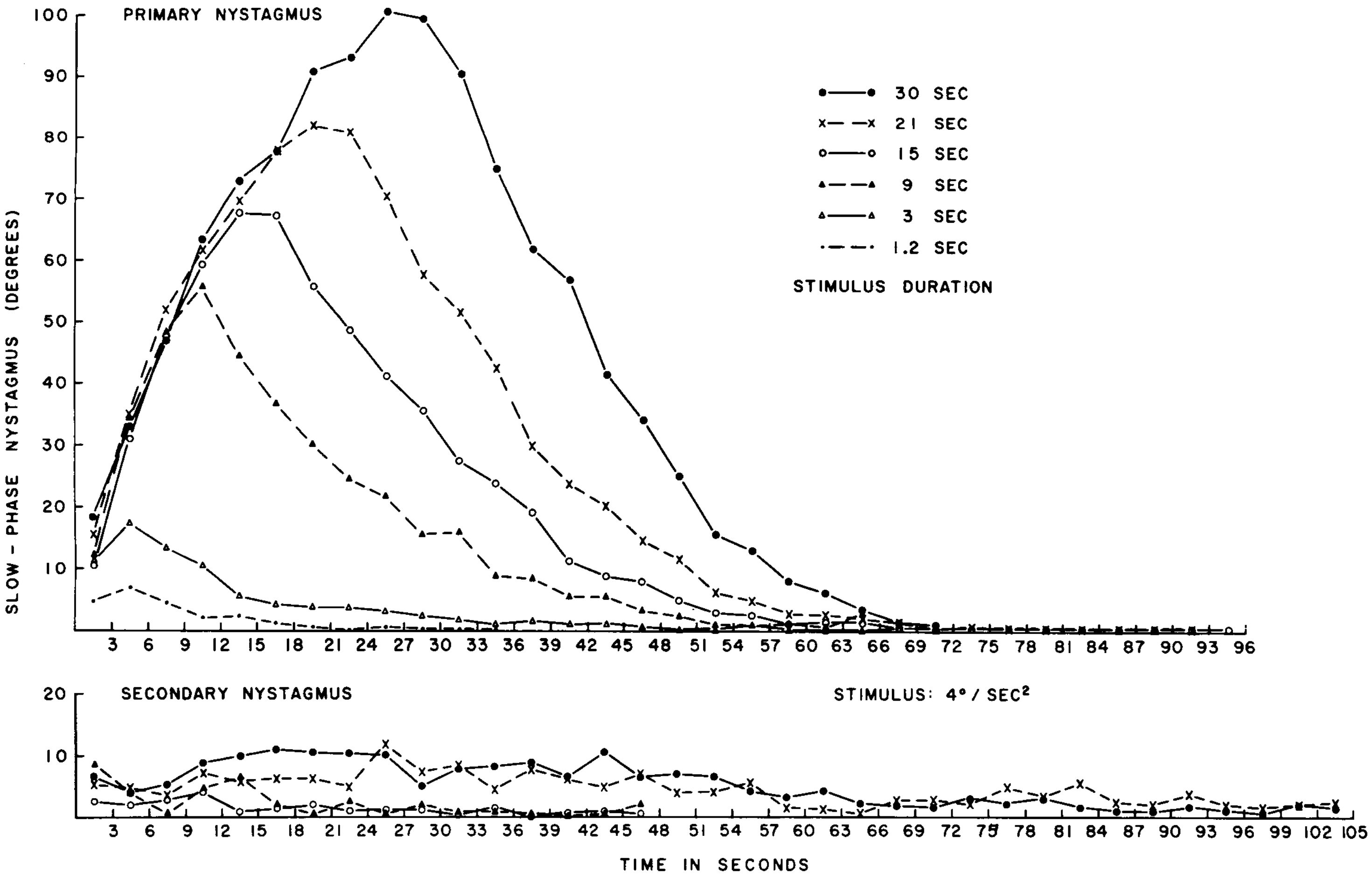

Figure 2

Time-Course Plots of Slow-Phase Eye Displacement per 3-sec Interval for 12 Human Subjects Exposed to Six Stimulus Durations of 4°/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.

fairly well in its temporal characteristics with the human subjective response. This is shown in Figure 3 where the subjective responses (mean duration of turning sensations) from the present study are presented along with subjective data obtained in a previous study (13). In the earlier study 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 are also matched fairly well by the change in temporal characteristics of nystagmus in the cat, also shown in Figure 3. Reference to Tables II and III 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-second stimuli, and several subjects gave no secondary response to the 30-second 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 II and III suggest that the number of beats of secondary nystagmus is more closely related to the duration of primary poststimulus nystagmus than to the duration of the stimulus. This is in contrast to the maximum slow-phase velocity of secondary nystagmus which seems to be related to the stimulus duration, at least in the cat (see Figure 1). The decline in number of secondary beats with stimuli longer than fifteen seconds 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 a substantially different rate of decline of nystagmus (lower time constant) than man for comparable stimuli (see Figure 4). It also appears that slope of nystagmus decline for both man and cat changes as a function of stimulus duration, the longer stimuli producing poststimulus nystagmus with a higher rate of decay (lower time constant).

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

Table III

Humans: Measures of Primary Nystagmus Following Termination of Each Stimulus*

	Time from End of Stimulus to End of Primary Nystagmus (sec)					
Subject	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	27.3
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	-	-	-	-	-	26.1
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	36.1	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 =	#	#	36.8	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	27.5
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

*Each response value is a mean of responses to an acceleration and a deceleration stimulus of 4 deg/sec^2 for indicated durations.

#Too few scores on which to base a mean.

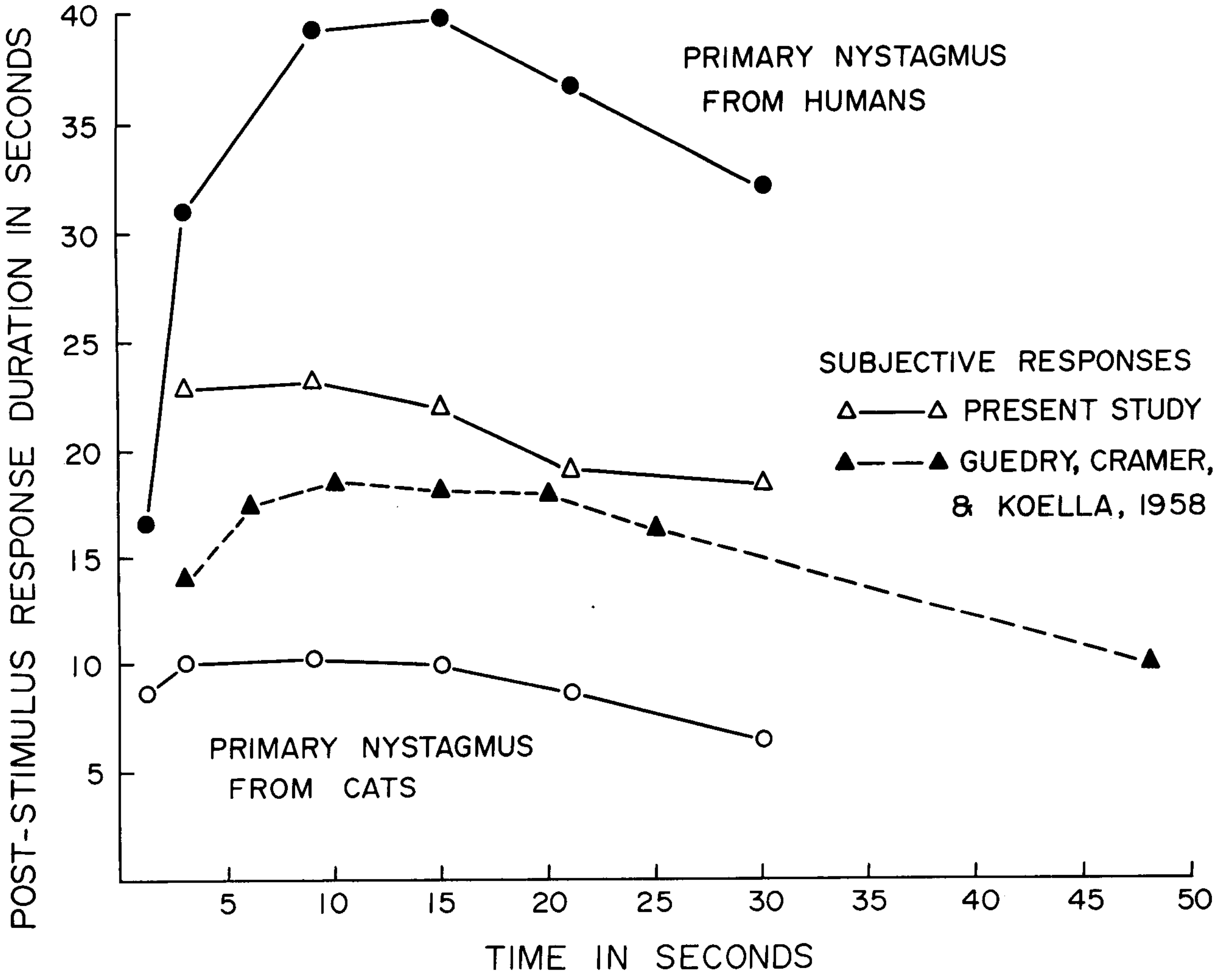

Figure 3

Duration of the Post-Stimulus Subjective and Nystagmic Reactions Obtained in This Study Are Compared with Subjective Data from an Earlier Study

The abcissa 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.

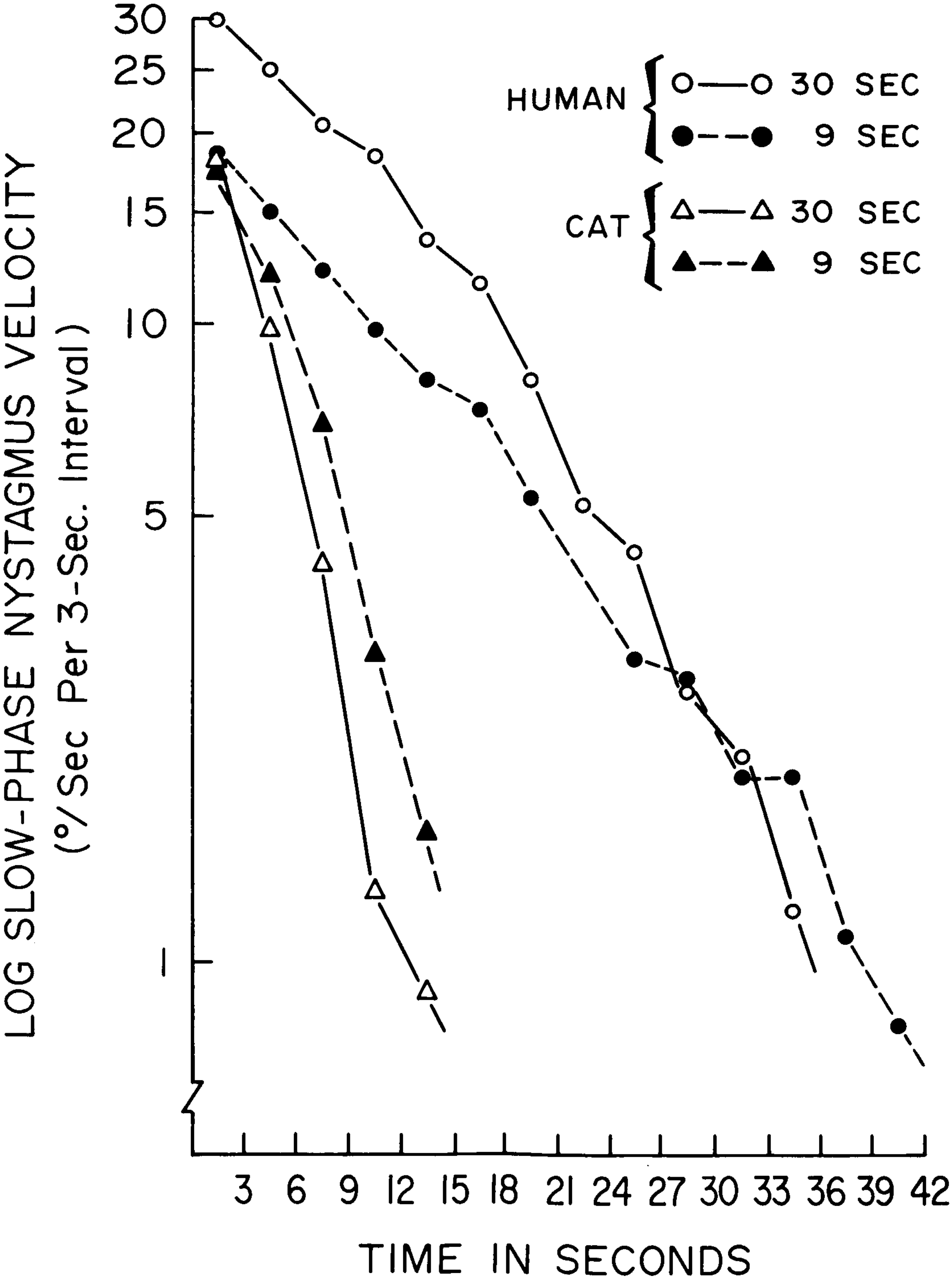

Figure 4

Log Plots of Slow-Phase Eye Velocity Following Two Stimuli 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.

nystagmus in alert men did not decline during prolonged angular acceleration; the rate of decline of primary vestibular nystagmus after application of 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 deviated 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 poststimulus 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 slightly underdamped, contrary to the common supposition, would explain a secondary response, but this seems at variance with much of the evidence for the overdamped torsion pendulum analogy of van Egmond, Groen, and Jongkees (21) 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 al*. have proposed (21) that events within the endorgan, either bioelectric, biochemical, or plastic change within the cupula, could account for secondary responses, and this possibility cannot be ruled out. Lowenstein (16) has reported that increasing cupula deflection in elasmobranch initiates neural activity "...in one after the other previously silent units..." which often adapt themselves rapidly. Adrian (1) and recently Melvill Jones (17), recording from the vestibular nuclei in cats, found little evidence for rapid adaptation. However, Cappel (3) 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). It does not seem reasonable to attribute the decline of the one response to a peripheral suppression of sensory inflow when the other response, nystagmus, did not show a comparable decline. (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 Bergstedt (2) have evidence which implicates the central nervous system in secondary responses. Prolonged primary responses induced by unilateral caloric stimulation should provide an opportunity for adaptive changes within the cupula; yet Aschan and Bergstedt (2) 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 nystagmus.

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 theoretical (11) 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 departures from expected results signify a range of unnatural stimuli which are not accurately followed due either to 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 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.

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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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