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ADAPTATION TO VESTIBULAR DISORIENTATION

V. Eye-Movement and Subjective Turning Responses to Two Durations of Angular Acceleration

William E. Collins, Ph.D.

Fred E. Guedry, Jr., Ph.D.

Approved by

J. Robert Dille, M.D.
Chief, Civil Aeromedical Institute

Released by

P. V. Siegel, M.D.
Federal Air Surgeon

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Dr. Collins is Chief, Psychology Laboratory, Civil Aeromedical Institute; Dr. Guedry is Chief of Experimental Psychology, Research Department, USN Aerospace Medical Institute, Pensacola, Florida.

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I. Introduction.

During prolonged angular acceleration, inertial torque deflects the cupula but the deflection is eventually balanced, primarily by the cupula's elastic restorative force. Assuming that cupula displacement from its position of static equilibrium controls the magnitude of vestibular reactions, a prolonged angular acceleration should, according to the "Torsion-Pendulum" theory[11], yield an increasing response for about 20–30 sec; this response level should be maintained without decline as long as the angular acceleration continues. Several authors[9,10,13,18,19] have reported that the subjective velocity rises and declines during prolonged angular acceleration, contrary to theoretical expectations. Guedry & Ceran[13] showed that the temporal period required for the subjective reaction to peak (and then decline) was about constant (27 sec) for angular accelerations ranging in magnitude from 0.5 to 2°/sec^2. Subsequent experiments (Guedry & Cunat, unpublished) showed this to be true for stimuli up to 4°/sec^2.

The present experiments seek to compare cat and man in regard to several characteristics of the nystagmic response elicited by two durations of a 4°/sec^2 angular acceleration.

II. Methodology.

A. Cats

Apparatus. The Huffman Rotation Device[6] located in a light-proof room, was used to produce acceleration programs. Animals were tested on the rotator in pairs with their heads at the center of rotation. One cat box was secured to runners on the turntable and the second box was secured to a framed tier arrangement above the first box.[7]

Restraint. Cats were restrained by the method of Henriksson, Fernandez, and Kohut.[16] Three or more days prior to testing, the animals were anesthetized and holes were drilled transversely through their canine teeth. At the same time, fur around the ocular orbits was shaved off and a guideline for positioning the head was drawn with washable ink from the canthus to the tragus on each side. For testing, each animal was wrapped in a towel and placed in a cat box. A strand of piano wire was inserted through the holes in the canine teeth. The wire was held securely and the head of the animal was positioned by means of an adjustable device on the front of the box.

Recording. For recording horizontal components of eye movements, needle electrodes were inserted by the outer canthi. Vertical components were obtained by means of surface electrodes taped above and below the left eye. The recorder was an Offner Type R Dynograph with 3-sec time constants used in amplification. Prior to testing, animals were placed in an optokinetic stimulator; a drum speed of 24°/sec was used to obtain data for calibration purposes.

B. Human Subjects

Apparatus. A Stille-Werner RS–3 rotating chair, situated in a light-proof room, provided the acceleratory stimuli for the human subjects.

Recording. A pair of surface electrodes, taped by the outer canthi of the eyes, detected horizontal eye movements, while a second pair was positioned above and below the left eye for the recording of vertical eye movement. An Offner Type T polygraph with a 3-sec time constant was used in amplifying and recording the eye movement signals. Eye calibrations were obtained prior to each test by means of a calibration chart located on one wall of the rotation room.

III. Procedure.

Each of eight cats and eight human subjects received 2 angular accelerations (for 8.4 and 36 sec) stimulating the lateral semicircular canals.

The same durations were used for the vertical canals. Stimuli were 4°/sec² accelerations and decelerations separated by 54 sec of constant velocity for cats and by 120 sec of constant velocity for humans. In cats, vertical canal stimulation was accomplished by placing each animal on its right side to locate its sagittal plane at the center and in the plane of rotation; human subjects leaned forward with the head turned to place the sagittal plane of the skull in the plane (and at the center) of rotation. A biteboard and head rest assisted in this positioning. Stimuli were presented in a counter-balanced order as indicated in Table 1.

Neither the cats nor the human subjects had been used in previous vestibular experiments. For the humans, this necessitated instruction regarding the signalling of subjective events without actual practice in making such judgments; they reported onset and cessation of apparent rotation by means of a signal key.

TABLE 1. Order of stimulus presentation. All trials comprised stimuli of 4°/sec². Duration of the stimulus was either 8.4 or 36 seconds. L and V refer, respectively, to lateral and vertical canal stimulation.

Human Subjects	*Cats*	*Rotation Direction*	*Trials* 1	2	3	4
Or & Wa	100 & 101	CW	8.4 L	36.0 L	8.4 V	36.0 V
Nu & Jo	102 & 103	CCW	36.0 L	8.4 L	36.0 V	8.4 V
Pe & Me	104 & 105	CW	8.4 V	36.0 V	8.4 L	36.0 L
Fr & Ma	106 & 107	CCW	36.0 V	8.4 V	36.0 L	8.4 L

IV. Results and Discussion.

The 8 animals received only 4 trials (2 lateral and 2 vertical canal stimulations) on the first day. Some examples of recorded nystagmus appear in Figure 1. The critical portion of the response for several purposes of this study began at the *end of each stimulus*. Thus, time measurements were 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 also tabulated. These data appear in Table 2. In 47 of the 48 comparisons, the primary post-stimulus responses to the 8.4 sec stimulus exceeded those of the 36 sec stimulus.

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 decleration stimulus. Stimuli were 4°/sec² for either 8.4 or 36 seconds.

	Time From End of Stimulus to End of Primary Nystagmus (Sec)				*Time From End of Stimulus to Start of Secondary Nystagmus (Sec)*				*Beats of Primary Nystagmus After End of Stimulus*			
	Lateral		*Vertical*		*Lateral*		*Vertical*		*Lateral*		*Vertical*	
Cat	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*
100	9.2	2.5	6.5	0.5	12.9	5.7	11.1	3.4	8.8	2.8	9.0	1.0
101	11.4	7.0	7.9	7.0	14.4	8.7	9.1	9.4	14.8	10.0	11.5	7.8
102	3.2	0.5	25.7	5.7	6.0	0.9	28.3	9.1	3.3	0.5	18.5	4.0
103	4.9	4.4	8.8	4.2	8.1	6.3	18.1	6.2	3.5	1.5	7.5	3.5
104	10.7	5.4	8.2	3.1	12.0	6.6	10.9	3.9	8.8	2.0	7.0	2.5
105	13.8	6.9	13.6	3.0	15.8	10.4	14.6	4.3	14.5	8.0	10.0	2.8
106	11.5	5.7	6.0	4.8	14.7	7.0	7.7	7.2	10.0	4.5	5.5	4.5
107	10.9	8.2	6.0	−1.5*	14.6	11.0	17.5	3.7	7.5	6.0	6.5	1.0
M=	9.5	5.1	10.3	3.4	12.3	7.1	14.7	5.9	8.9	4.4	9.4	3.4

* Nystagmus ended during stimulus.

Plots of the complete nystagmic responses to the 8.4 and the 36 sec stimuli appear in Figure 2. Slow-phase output was scored by summing the vertical displacements of beats from peak to base-line for successive 3-sec intervals. Greater output of primary nystagmus is evident for the lateral canals, as compared with the vertical canals, for both stimulus durations. For the 8.4 sec stimuli, primary nystagmus increased throughout the stimulus period for both the "horizontal" and "vertical" curves. For the 36 sec stimulus, there was a marked peaking in the response to stimulation of the vertical canals during the 15–18 sec interval, and a steady decline of that response throughout the remainder of the stimulus. For stimulation of the lateral canals during the 36 sec stimulus, peaking occurred in the 18–21 sec interval and was followed by a lesser decline than that noted for the vertical canals.

Secondary nystagmus was also plotted in Figure 2. With only one exception (the 8.4 sec stimulus to the vertical canals for cat No. 100), scorable secondary nystagmus was obtained from each cat for each stimulus condition. For both vertical and lateral canal responses, the 36 sec stimuli produced greater secondary responses than did the 8.4 sec stimuli. In addition, horizontal secondary nystagmus showed greater output than vertical secondary nystagmus by amounts proportional to differences in their respective primary reactions. Further, the mean peak of the secondary response occurred 21–24 sec after the end of the 8.4 and 36 sec stimuli for horizontal nystagmus, and 15–31 sec after the 8.4 and 36 sec stimuli for vertical nystagmus.

To pursue further the relationship of secondary to primary nystagmus and the effects of prolonged stimuli on those responses, six of the animals were given, one day later, a series of 15 trials stimulating the lateral canals with the $4°/sec^2$ stimulus for 36 sec duration. Tracings for trials 1, 5, 10, and 15 were scored and the data plotted in Figure 3. With repeated stimulation, a marked depression of both the primary and secondary response curves occurred, peaking of the response was followed by a decline in nystagmic output during the remainder of the stimulus, and the peaks of both primary and secondary nystagmus shifted toward earlier occurrences.[5]

A. Human Subjects

Eight human subjects (4 males and 4 females) were given stimulations identical to those administered to the cats. Nystagmus data were also scored similarly and appear in Table 3. Some examples of nystagmus tracings are presented in Figure 4. In addition, duration of the sensation of turning was calculated from the *end of each stimulus* to the end point of the sensation (Table 4).

In 20 of the 48 comparisons (Table 3), human responses to the 36 sec stimulus exceeded responses to the 8.4 sec stimulus (9 of these cases were for the "number of beats" measure) and,

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 $4°/sec^2$ for either 8.4 or 36 seconds.

	Time From End of Stimulus to End of Primary Nystagmus (Sec)				*Time From End of Stimulus to Start of Secondary Nystagmus (Sec)*				*Beats of Primary Nystagmus After End of Stimulus*			
	Lateral		*Vertical*		*Lateral*		*Vertical*		*Lateral*		*Vertical*	
Subject	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*	*8.4*	*36*
Nu	24.7	18.9	21.1	7.6	32.9	26.5	55.2	13.4	18.5	14.5	15.0	9.0
Or	29.8	34.7	16.1	26.5	32.0	36.6	9.8	9.0	92.0	61.5	25.5	23.0
Me	32.0	25.4	16.0	14.6	38.6	32.1	24.2	16.5	25.0	24.5	13.0	9.5
Wa	42.4	33.0	8.5	10.5	48.1	38.6	13.6	14.9	23.0	32.5	5.0	10.5
Pe	18.2	23.2	6.2	11.2	21.6	24.5	9.8	19.2	9.5	21.0	2.5	9.5
Fr	36.2	30.4	22.4	9.0	39.8	30.1	15.8	14.5	38.5	45.5	16.0	13.0
Jo	37.1	36.1	15.8	4.9	36.6	32.6	----	8.0	36.0	47.5	6.5	7.0
Ma	41.0	38.8	9.4	13.7	41.4	43.0	20.2	17.1	54.5	77.5	7.5	10.5
M=	32.7	30.1	14.4	12.3	36.4	33.0	21.2	14.1	37.1	40.6	11.4	11.5

although the mean group data for "duration of primary nystagmus" and for "time from end of stimulus to start of secondary nystagmus" were longer for the 8.4 sec stimulus, the differences were slight. Mean number of beats of primary nystagmus following stimulus termination actually favored the 36 sec over the 8.4 sec stimulus, but the differences were not significant. Thus, results obtained from the cats, in which the post-stimulus nystagmic responses to the 8.4 sec stimulus consistently exceeded those of the 36 sec stimulus, were not borne out in the data from human subjects.

TABLE 4. Time in seconds from end of each rotatory stimulus to end of subjective turning experience for uuman subjects. Each value is a mean for an acceleration and a deceleration stimulus. Stimuli were 4°/sec² for either 8.4 or 36 seconds.

	Lateral Canals		*Vertical Canals*	
Subject	8.4	36	8.4	36
Nu	----	----	----	----
Or	----	29.5	12.5	9.3
Me	34.5	12.4	44.0	9.2
Wa	27.8	14.9	10.4	23.7
Pe	11.0	6.7	7.7	2.0
Fr	23.1	14.3	11.5	28.6
Jo	20.4	12.4	19.9	−1.3*
Ma	7.7	3.1	7.4	−15.1*
M =	20.8	13.3	16.2	8.1

*Subjective turning experience ended during stimulus.

Human subjective data (Table 4), in 11 of 13 comparisons (3 comparisons were not obtained), showed that the 8.4 sec stimulus resulted in sensations of longer duration after termination of angular acceleration than did the 36 sec stimulus. For two subjects the sensation to vertical canal stimulation ended during the 36 sec stimulus.

Time plots of the nystagmus recorded during the two stimulus conditions appear in Figure 5. Responses from the lateral canals were of greater magnitude than those from the vertical canals. No clear peaking or decline in output during the stimulus appeared for either set of canals. Secondary nystagmus was plotted in the same figure. However, of the 8 subjects, 6 gave no scorable secondary responses to the 8.4 sec lateral canal stimulus, 5 gave none to the same stimulus applied to the vertical canals, 3 gave none to the 36 sec vertical canal stimulus, and one gave no scorable secondary nystagmus to the 36 sec lateral canal stimulus. Thus, in two general respects, human data differed from cat data: 1) humans did not show a rise and decline during prolonged (36 sec) stimulation whereas the cats did; 2) little or no secondary nystagmic reactions to the 8.4 sec stimuli were demonstrated by humans whereas cats consistently gave such responses.

Arousal. The importance of arousal on nystagmic responses was noted earlier and has been examined in considerable detail elsewhere.[3] To assure reliability of the present data with regard to this factor, a second group of 10 cats was treated with d-amphetamine in accordance with procedures described by Crampton and Brown.[8] Each animal received 4 trials with each trial comprising an acceleration stimulus of 4°/sec² for 36 sec, 2 min of constant velocity, and a subthreshold deceleration (0.15°/sec²). The first two trials were always stimulation of the lateral canals; the remaining two trials involved vertical canal stimulation. Trials were alternately CW and CCW. Half the animals began with CW rotation; the remaining 5 began with CCW rotation. Data from CW and CCW accelerations were similar for the horizontal and the vertical nystagmus curves and, therefore, were averaged. The mean response curves for the 10 animals appear in Figure 6 and demonstrate the same type of decline during stimulation and almost identical transition points from primary to secondary nystagmus as those presented by the undrugged cats. Vertical nystagmus again shows a more pronounced decline during stimulation than does horizontal nystagmus. Some supportive neural data for this decline of response during stimulation of the cat has been presented by Cappel[2] who showed plots of single neural unit activity during a prolonged angular acceleration and reported a rise and decline of firing during the stimulus period.

A reliability check of the findings for humans was accomplished by exposing 4 males and 4 females, all previously untested, to stimulus conditions (4°/sec² for 36 sec) identical to those administered to the other human subjects. Half of the males and females received CW stimulation, the remaining half received CCW rotation. Four trials were administered, two each for the lateral and vertical canals. The first two trials always employed mental arithmetic (MA) as

an arousal task[3], while in the last two trials, the Key Press (KP) technique of estimating subjective velocity was used to maintain alertness. With the KP technique, the subjects attempted to signal successive angular displacements of 90°. Table 5 contains an outline of the test procedures for this reliability check. Nystagmus data for acceleration and deceleration and for the two tasks showed no evidence of a fall-off in response during stimulation, and the primary-to-secondary nystagmus transition points were almost identical to those obtained under the first set of conditions. The data were thus combined and curves depicting horizontal and vertical nystagmus were plotted in Figure 7. As in the first group of human subjects, no clear evidence for a decline of response during the stimulus is evident. However, the vertical nystagmus time-plot does show considerable irregularity as compared with horizontal nystagmus data. Thus, the differences between man and cat that were obtained from the first groups of subjects were confirmed with different subjects and under conditions in which the arousal variable was manipulated.

TABLE 5. Order of stimulus presentation for human subjects used in the reliability check. Arousal of subjects was controlled by Mental Arithmetic and Key Press tasks. All trials comprised accelerations and decelerations of 4°/sec² for 36 sec separated by 2 min of constant velocity.

Subjects		*Rotation*	*Mental Arithmetic*		*Key Press*	
Male	*Female*	*Direction*	*Trial 1*	*Trial 2*	*Trial 3*	*Trial 4*
A	W	CW	Lateral	Vertical	Vertical	Lateral
B	X	CCW	Lateral	Vertical	Vertical	Lateral
C	Y	CW	Vertical	Lateral	Lateral	Vertical
D	Z	CCW	Vertical	Lateral	Lateral	Vertical

It has been reported that vestibular nystagmus rises and declines, like the subjective reaction, during constant angular acceleration.[1,17,20,21] However, Guedry & Lauver[15] demonstrated that the nystagmic reaction in man did not decline during prolonged constant angular acceleration if the subjects were required to signal estimates of angular displacement. Occasionally, however, a subject would yield a rise and decline in the nystagmus response similar to the subjective responses in earlier experiments (see Figure 4 in Guedry & Lauver[15]). To check the possibility that arousal accounted for the variety of findings, Collins & Guedry[4] required subjects, during prolonged angular accelerations, to perform mental tasks, which would maintain mental activity independent of the subjective perception of rotation. Subjects were required to make arithmetic computations throughout the vestibular stimulation and post-stimulation periods. Results showed again that nystagmus first increased and then remained constant during constant angular acceleration. Following the termination of stimulation, nystagmus decayed about as expected from the "torsion pendulum" theory[11], although rates of decay were not calculated. The same subjects, when allowed to relax, occasionally showed a rise and decline of nystagmus during constant stimulation, and a rapid decay of response on termination of the stimulus. The present experiments confirm the fact that nystagmus does not decline during prolonged angular acceleration in alert human subjects, although such declines appear to occur in cats.

In cats, time to *onset* of secondary nystagmus was inversely related to duration of the stimulus. The earlier *onset* of the secondary reaction cannot be attributed to loss of arousal. This result strongly suggests that the decline in primary nystagmus during and after the longer stimuli resulted from a counteracting process which reduced the intensity and duration of the primary nystagmus and then became evident as an early secondary nystagmus. Data from humans have shown that as the duration of a constant angular acceleration is increased beyond certain time limits, the duration of the subjective after-responses becomes shorter and shorter.[12,14] Nystagmic reactions in cats showed similar effects and, in these respects, more closely resembled the subjective reactions of man than they did the nystagmus of man.

V. Summary.

Recordings of ocular nystagmus were obtained from a group of cats and a group of human subjects to $4°/sec^2$ angular accelerations of 8.4 sec and of 36 sec duration. Lateral canals and vertical canals were stimulated on separate trials. Results showed that the output of both primary and secondary nystagmus was greater for lateral canals. In cats, both lateral- and vertical-canal responses to the 36 sec stimuli peaked after 15–21 sec of angular acceleration and this was followed by a steady decline. Declines were not apparent in nystagmus of human subjects. A further test of these findings was conducted by manipulating arousal variables; human subjects were given special tasks and cats received d-amphetamine. Essentially the same results were obtained as described above. Other differences between the two groups were noted. Cats consistently demonstrated secondary nystagmus whereas humans did not. After termination of acceleration, primary nystagmus from cats lasted longer and exhibited a greater number of eye movements following the 8.4 sec stimulus than following the 36 sec stimulus; this consistency was not evident in humans. However, for humans the sensation of motion following termination of acceleration was of longer duration for the 8.4 sec stimulus than for the 36 sec stimulus. In this regard, nystagmus from cats resembled the subjective reactions of man more than they did the nystagmus of man.

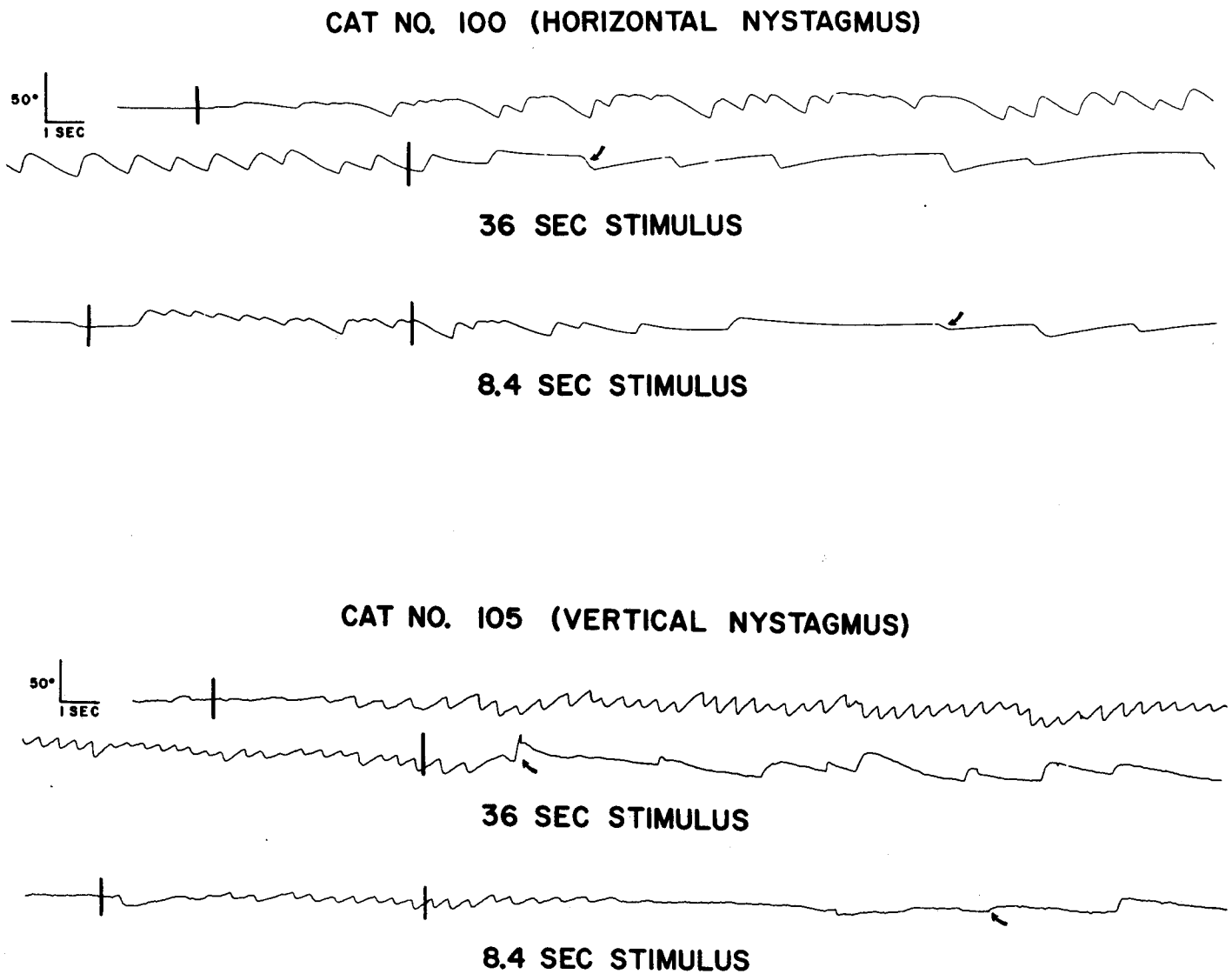

FIGURE 1. Nystagmus recorded from two cats for two durations of a 4°/sec² angular acceleration. Responses to stimulation of the lateral canals (Cat No. 100) and the vertical canals (Cat No. 105) are presented. Vertical bars through the tracings demarcate the stimulus periods; arrows indicate the start of secondary nystagmus. Note the longer poststimulus primary nystagmus and the later onset of secondary nystagmus for the shorter duration of acceleration.

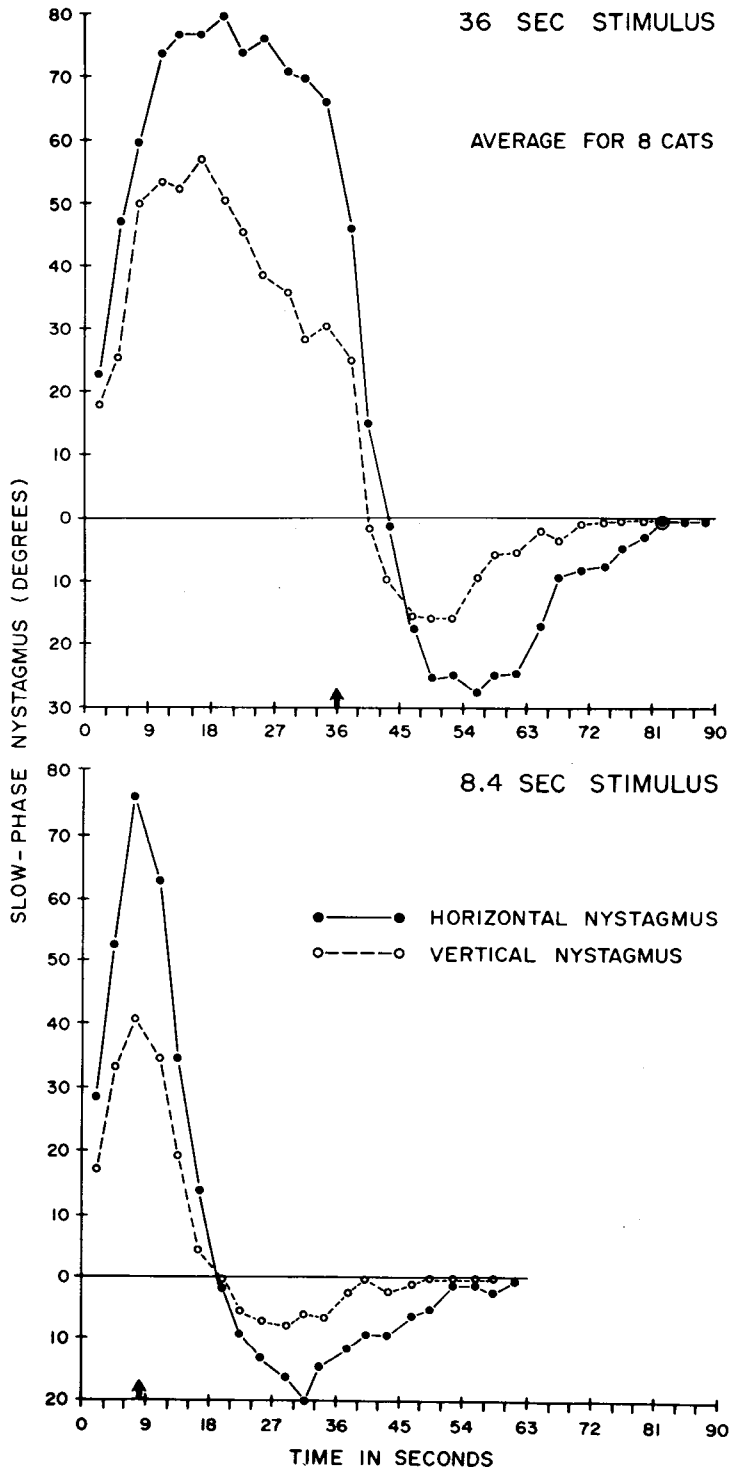

FIGURE 2. Time-course plots of slow-phase eye displacement in 3-sec intervals for 8 cats. Arrows indicate termination of acceleration. Points above the zero line represent primary nystagmus; points below the zeroline represent secondary nystagmus. In the upper graph, a clear peaking and decline of nystagmus during the acceleration is evident for responses to both lateral- and vertical-canal stimulation. In the lower graph (8.4 sec stimulus), 3-sec intervals were marked off from the *end* of the stimulus (thus the first "3-sec" interval represents response during only 2.4 sec of stimulus). Total output of both primary and secondary nystagmus is consistently greater for the lateral canals.

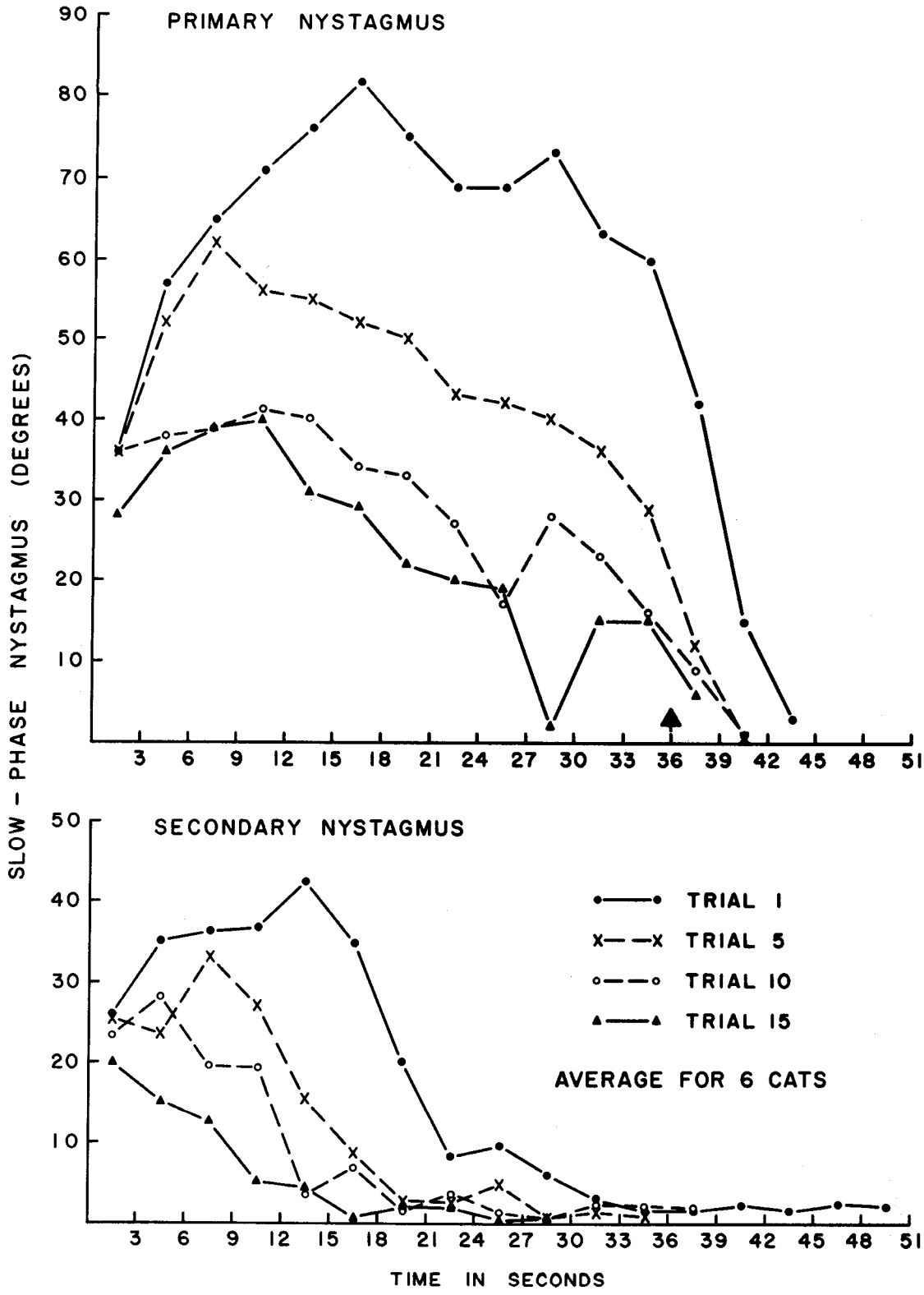

FIGURE 3. Time-course plots of slow-phase eye displacement for trials 1, 5, 10, and 15 of the habituation series. With repeated trials there occurs a depression of output with early peaking followed by rapid declines during the accelerations. Effects are similar for both primary and secondary nystagmus.

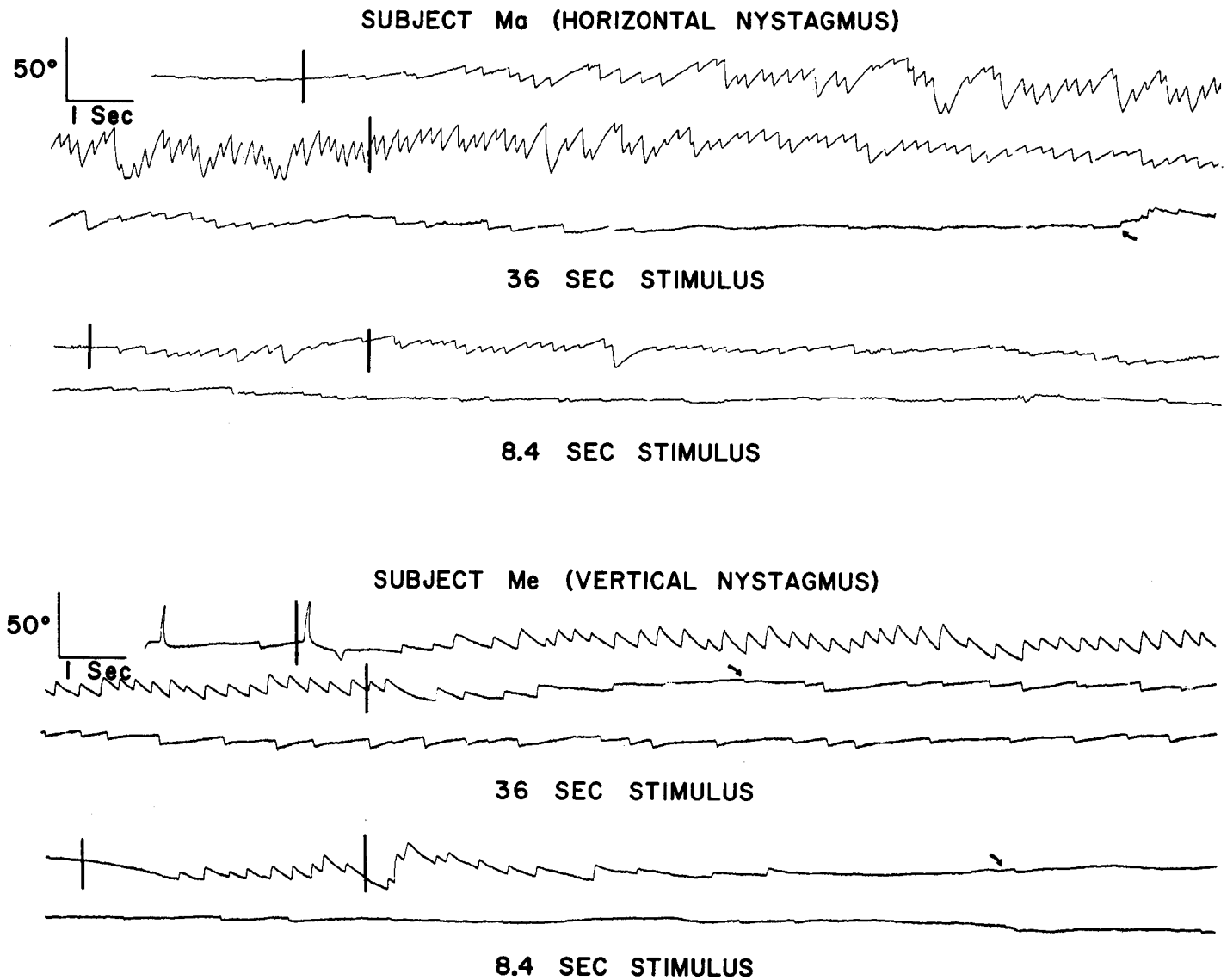

FIGURE 4. Nystagmus recorded from two human subjects for two durations of a 4°/sec² angular acceleration. Responses to stimulation of the lateral canals (Subject Ma) and of the vertical canals (Subject Me) are presented. Markings are the same as in Figure 1. The clearly longer responses of the lateral canals to the shorter stimulus duration which were obtained from cats are not so evident here (compare Subject Ma data with Figure 1). Subject Me (vertical nystagmus) was atypical of human subjects in demonstrating clear and consistent secondary nystagmus with tracings closely resembling those obtained from cats.

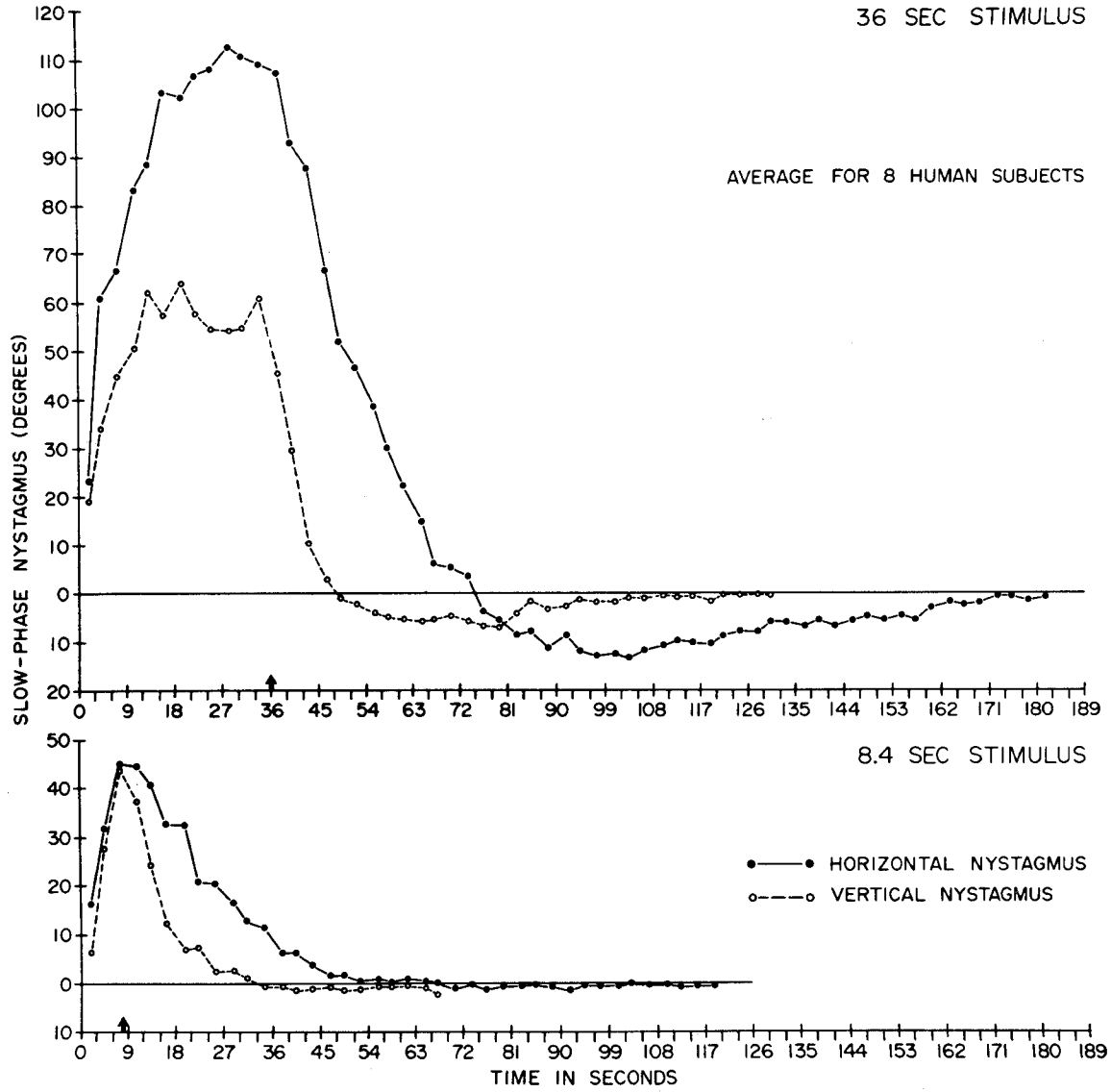

FIGURE 5. Time-course plots of slow-phase eye displacement in 3-sec intervals for 8 human subjects. Markings are the same as in Figure 2. Total output of both primary and secondary nystagmus is greater for the lateral canals. In the upper graph, no clear peaking and subsequent decline of nystagmus during the acceleration is evident, although a large dip appears in the data for the vertical canals (compare with Figure 7).

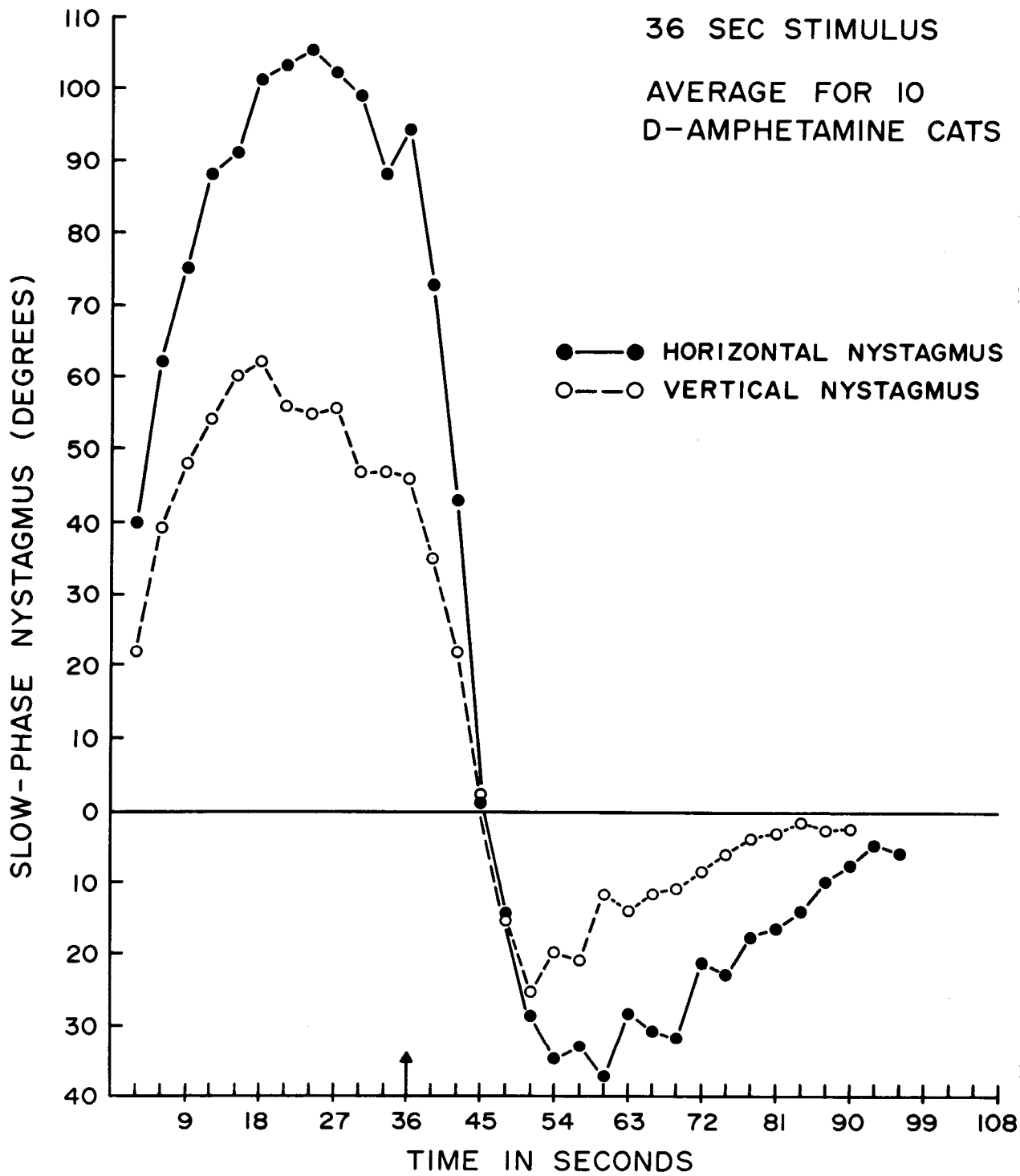

FIGURE 6. Time-course plots of primary and secondary nystagmus in 3-sec intervals for cats treated with d-amphetamine. Similar to results obtained from undrugged cats, a peaking and decline of the response during the 36 sec stimulus (4°/sec²) is evident for both lateral- and vertical-canal stimulation (compare with Figure 2).

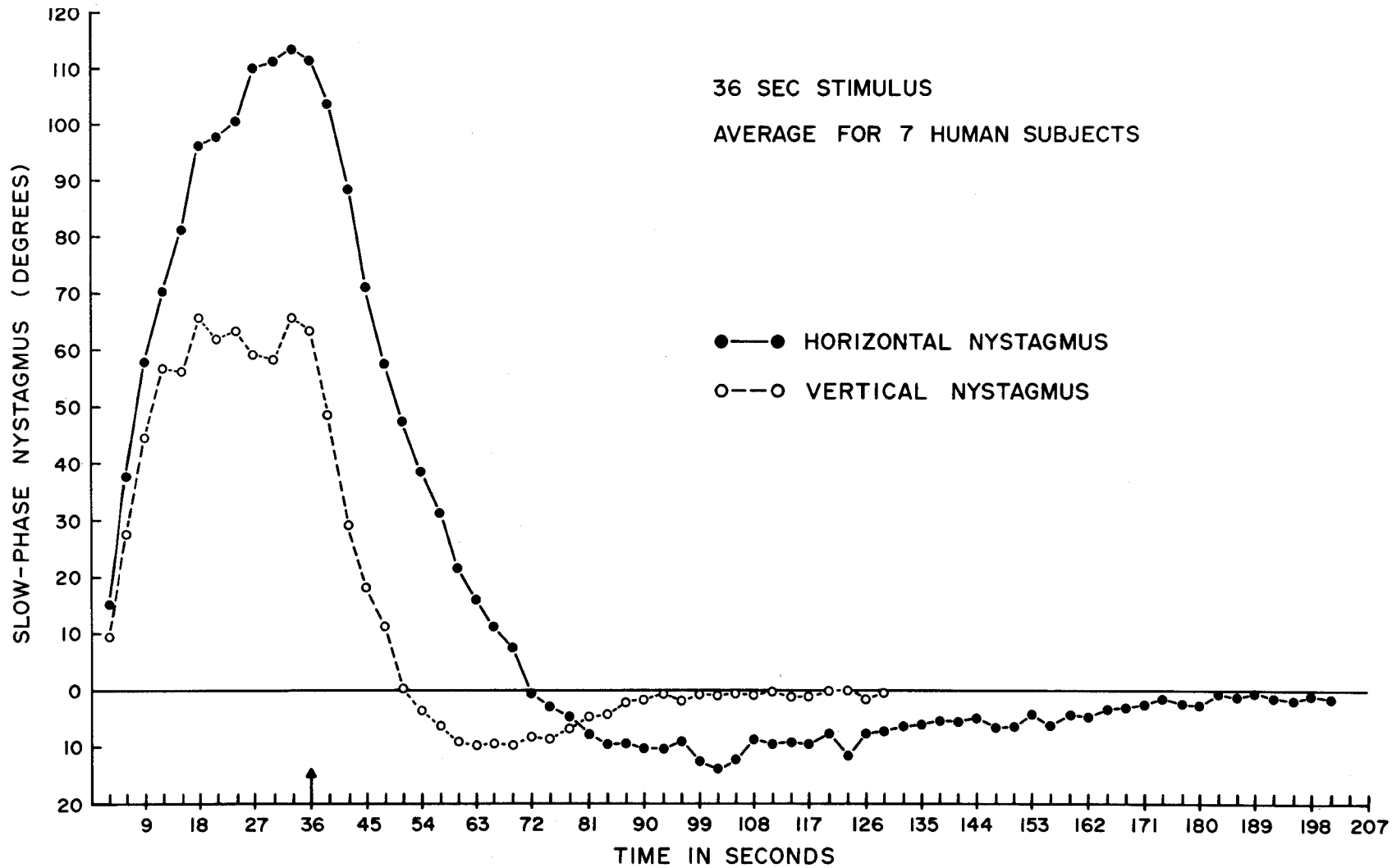

FIGURE 7. Time-course plots of primary nystagmus in 3-sec intervals for a second group of humans who were given instructions influencing arousal during the tests. Stimuli were 4°/sec² angular accelerations for 36 sec. Each point is an average of two task-trials (metal arithmetic and key pressing) for each of the 8 subjects. Similar to results obtained under other arousal conditions (compare with Figure 5), no peaking and subsequent decline of nystagmus during accelerations is evident. One female subject was excluded from the average curves due to the presence of a spontaneous nystagmus which particularly affected scoring of secondary responses.

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