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SOME CHARACTERISTICS OF OPTOKINETIC EYE-MOVEMENT PATTERNS: A COMPARATIVE STUDY

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I. Problem.

Optokinetic nystagmus is an ocular reaction which occurs when a series of moving objects crosses the visual field, or when an observer moves past a series of objects.[30] The eyes involuntarily track the visual stimulus to the edge of the visual field or to the limit of comfortable gaze, and then make a rapid corrective movement in the opposite direction;[3] they then fixate on a new stimulus, repeat the pattern of slow (following) and quick (return) movements, and thereby generate an ocular nystagmus.[21] Patterns of optokinetic nystagmus, although reportedly noted as early as 1825 by Purkinje while observing a crowd at a cavalry parade,[12] have long been associated with transportation; Helmholtz is cited as having mentioned in an 1866 article that the response was most readily seen when objects were observed from a train in motion.[12] Indeed, one of the common terms used to describe this response was "railroad nystagmus";[1 21] that term is still used although the same phenomenon occurs in watching the external world from moving airplanes, cars, and other vehicles. The eye-movement pattern is similar to that produced by head movements which stimulate the vestibular system; in this case, the pattern facilitates vision during ordinary earth-bound activities, but can cause blurring of vision during "pilot's vertigo."

In themselves, characteristics of optokinetic nystagmus are of significance. Wolfe,[32] for example, reported that a steady drop (adaptation) occurs in the following reaction of the human eye from the first few seconds of optokinetic stimulation throughout a 30-sec stimulus period. If so, the eye, within this short a period of time, would track at slower and slower velocities. In addition, certain types of work have been reported to produce an undesired occupational nystagmus. The most familiar of these is "miner's nystagmus"—a condition believed to be due to long periods of visual demand under very poor lighting conditions. Less well-known is the occupational nystagmus found many years ago for train dispatchers;[26] it appeared to be related to job tasks which required continual movement of the head and eyes over a busy dispatcher's train movement sheet, as well as continual movement of that sheet (sheet dimensions were 5–9 feet by 2–3 feet, ruled into approximately 4000 small rectangles related to stations, trains, and crews).

The relationship between characteristics of the optokinetic response to those of the vestibular reaction is also of importance. For example, a prominent feature of the vestibular nystagmus elicited from cats by means of angular acceleration is a secondary (reversed) response which occurs shortly after stimulus termination. The same eye-movement pattern occurs following optokinetic stimulation of rabbits[28] and of cats.[32] In man, secondary optokinetic reactions are considerably less frequent and tend to be quite weak; but many human subjects give vigorous secondary responses to vestibular stimulation. Moreover, optokinetic stimuli are frequently used to provide calibration data for vestibular studies (particularly with animals). Data published by Wolfe,[32] although not discussed in these terms, make questionable the use of this calibration procedure since he reported (a) steadily declining optokinetic responses from humans, and (b) an increasing response from cats from the first five seconds through the first 20 seconds of stimulation. The latter confirmed a finding obtained from rabbits by ter Braak.[2]

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*The animals used for this experiment were lawfully acquired and treated in accordance with the "Principles of Laboratory Animal Care" issued by the Animal Facilities Standards Committee of the Animal Care Panel, United States Department of Health, Education, and Welfare, Public Health Service, March 1963.

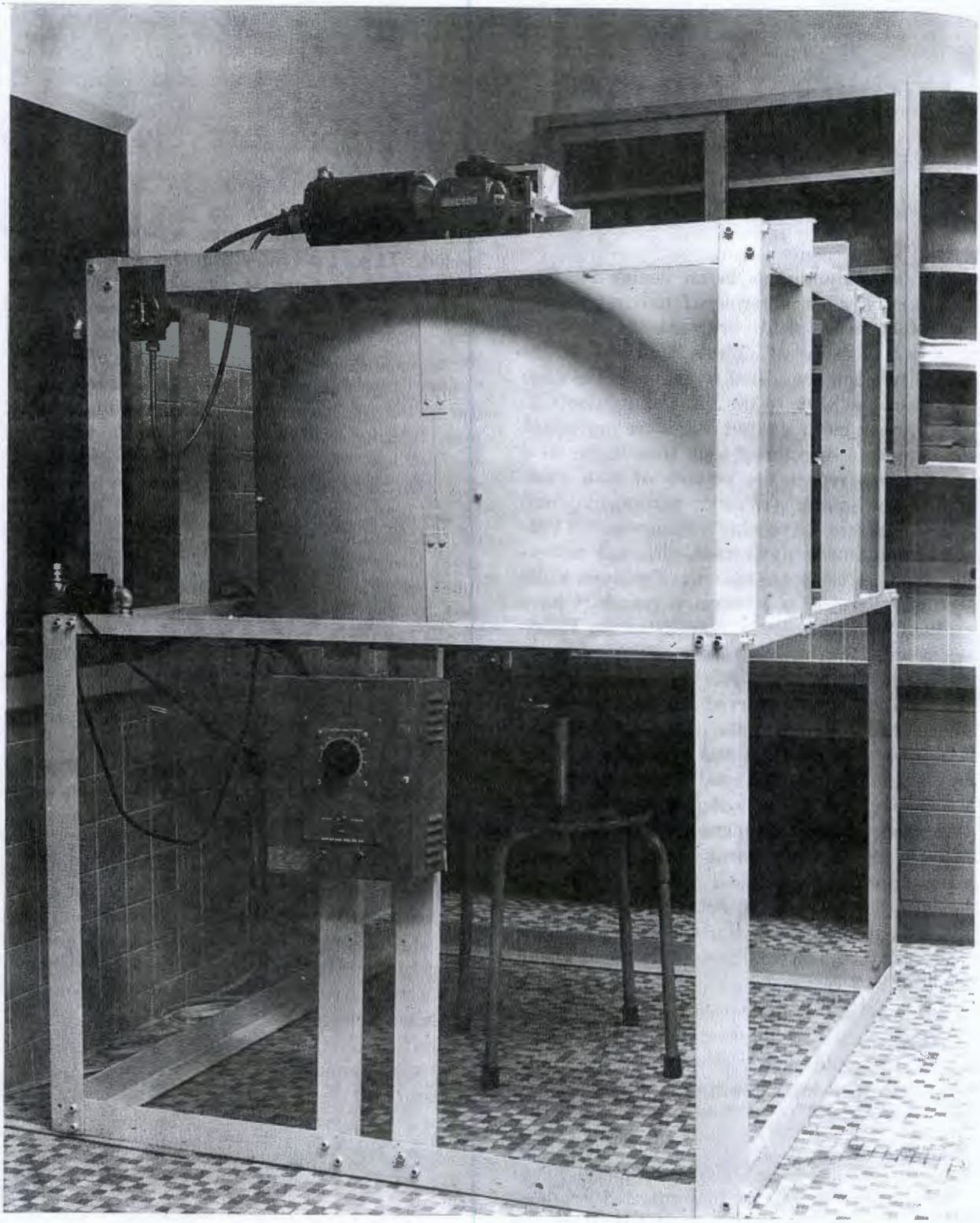


FIGURE 1. The CAMI optokinetic stimulator.

The present study was designed to examine in some detail the characteristics of optokinetic responses from men and animals, particularly with regard to the questions of adaptation and possible directional differences.

II. Method.

Subjects. Human subjects comprised five men and five women, nine of whom were between the ages of 21–29; one was age 37. All were laboratory personnel. All but one man and one woman were right-handed. The seven African parrots were young-adult birds which had been captured wild approximately six months prior to testing. The 22 cats and six dogs were mature, young animals, farm-reared and of mixed breed.

Apparatus. The optokinetic stimulator, located in a light-proof room comprised a steel drum supported by a steel frame (see Figure 1). The drum was four feet in diameter and two and one-half feet high, with its base 39 inches from the floor. The interior of the drum was painted white and to it were affixed vertical strips of black tape, each one inch in width and separated by two-inch intervals from adjoining strips. Each strip extended from the top to the base of the drum. Two small spotlights, attached to the ceiling of the drum, provided illumination. A Century DC motor with a variable speed control permitted rotation of the drum at a constant angular velocity of 24°/sec (4 rpm).

A modified, adjustable chair was positioned under the drum at the center of the turning axis. The chair had a removable back which permitted its conversion to an adjustable platform for use with animals. An attachment provided a headrest for human subjects.

Restraint. Cats and dogs were restrained by the technique described by Henriksson, Fernandez, and Kohut,[17] or by a modification of it.[9] Restraint of African parrots was accomplished by a procedure described elsewhere.[11]

Recording. Eye movements were recorded with an Offner Type T Electroencephalograph. With human subjects, surface electrodes were taped near the outer canthi for recording horizontal components of eye movements, and above and below the right eye for recording vertical responses. Surface electrodes were also used with cats for recording vertical ocular responses (needle electrodes were not effective[9]): fur around the left ocular orbit was shaved and the electrodes were taped in place.[7] Horizontal eye movements could be recorded from cats, dogs, and birds by means of needle electrodes. For the cats and dogs, the electrodes were inserted near the outer canthi of the eyes; for the birds, recording from each eye separately but simultaneously was accomplished by positioning electrodes on both sides of each eye. No attempt was made to record vertical nystagmus from the parrots or the dogs.

Calibration and Scoring. Human subjects were required to sweep their eyes from one marker to another on specially designed cards set at a standard distance (two feet) from each observer. The recorded displacement of the eyes was measured from the tracings in millimeters and converted to degrees/mm to serve as a calibration factor for measurements of optokinetic nystagmus. Eye movements for calibration purposes were obtained prior to each trial.

Optokinetic tracking during rotation of the drum served as the means of obtaining calibration factors for the birds, the dogs, and the cats. Tracings obtained during specified periods of drum rotation were measured, calibration constants determined, and the rest of the record scored and converted to degrees of eye movement with these constants.[4] The calibration factor for each parrot was obtained (in an earlier study) from measurements of each tracing during the 28–30 sec interval of stimulation, while for the dogs, the last available interval (16–18 sec) provided the calibration data. For cats, a block of 10 consecutive seconds of "good" recording (i.e., with little or no artifact, no apparent voluntary eye movement, etc.) on a given trial was used to obtain calibration factors for that trial.

All recordings were divided into 3-sec intervals for scoring purposes. Slow-phase nystagmus was scored by measuring the vertical distance, from peak to base line, of the slow-phase displacement of each nystagmic beat; these values were summed for each 3-sec. interval and converted to degrees as indicated above. Additionally, the number of beats within each interval was tabulated by simple counting procedures.

Procedure.

Parrots and Dogs. Data from the parrots[11] and dogs[10] were calculated from tracings obtained for calibration purposes in earlier studies. Only

horizontal nystagmus was elicited. All of the parrots were exposed to clockwise (CW) drum rotation followed by counterclockwise (CCW) stimulation after about one min of rest in illumination. Duration of the stimulus was always at least 30 sec and frequently was longer. For dogs, a similar procedure was followed but only 18 sec of response to CW stimulation was available for all six animals. During stimulation of parrots and dogs, the test room was in total darkness (to minimize possible distractions) with the exception of the miniature spotlights inside the optokinetic drum. At the conclusion of each trial, room lights were turned on and the drum was stopped. Afternystagmus in darkness was thus not recorded.

Cats. One group of 10 cats received 30-sec periods of stimulation to both CW and CCW drum rotation. For half of the animals, the CW condition occurred first; for the remaining five cats, CCW drum rotation was presented first. On a following day, five of the animals were tested for vertical optokinetic nystagmus for 30-sec periods. Since the elicitation of vertical responses required placing the animals on their sides, three cats were placed on their right sides and exposed first to CW then to CCW drum rotation; they were then placed on their left sides and again given CW and CCW stimulation. The remaining two cats were given the same stimulation but were placed on their left sides first. Two additional trials were conducted with these five cats; in both cases, the animals were on their right sides and the drum was rotated CW. During one such trial, the stimulus was applied for 15 sec; during the other, it was applied for 60 sec.

A different group of 12 cats was exposed to elicitation of horizontal optokinetic nystagmus for 15-, 30-, 60-, and 120-sec stimulus periods, presented successively and in that order on a single test day. CW drum rotation was used for six cats; CCW stimulation was applied to the remaining six.

Humans. Horizontal optokinetic nystagmus was elicited from five human subjects by CW rotation of the drum for 15-, 30-, 60-, and 120-sec periods, presented successively and in that order on a single test day. These trials were followed by a 30-sec optokinetic stimulus with CCW drum rotation. For the remaining five subjects, CCW stimulation was applied for the four stimulus durations, followed by a 30-sec CW trial. Vertical optokinetic responses were obtained the same way and for the same stimulus periods, but on a separate day to avoid possible fatigue effects.

General. The general procedure for testing the cats and the humans was similar. A restrained cat was positioned with its head under the axis of drum rotation, either in an upright position (horizontal nystagmus) or on its side (vertical nystagmus). All lights were extinguished immediately prior to the start of a trial. The drum was set in motion and, within 3–5 sec, the miniature spotlights inside the drum were turned on. At the conclusion of the stimulus period, the spotlights were turned off and the drum was stopped. Recording continued for an additional two min in total darkness. Intervals between trials comprised at least three min of rest in the lighted room. Timing was by means of a stopwatch.

Similarly, humans were seated either upright with their heads centered beneath the axis of rotation of the drum (horizontal nystagmus), or with their heads tilted to the side 90° and resting on the head rest (vertical nystagmus). The latter arrangement required the subjects to alter their usual sitting position to accommodate the lateral tilt of the head. Prior to each stimulus, calibration data were obtained as outlined above. The rest interval between trials was 3–5 min in the lighted room.

In all cases, attempts were made to keep the subjects alert throughout a trial. Auditory stimuli (e.g., hand clapping and shouting) were used with the dogs, birds, and cats. Human subjects were verbally encouraged periodically throughout each trial to maintain alertness, and were told to maintain their gaze in the "plane" of the black stripes (the black stripes appear "closer" to most subjects than does the white background).

III. Results.

Dogs. Both slow-phase and frequency plots in 3-sec intervals show a generally increasing output (Figure 2). The range of change, however, was not particularly great.

African parrots. Tracings for six parrots were of good quality for both CW and CCW drum rotation. Plots of both slow-phase data and response frequency (Figure 3) show that the nystagmic reaction increased for both meas-

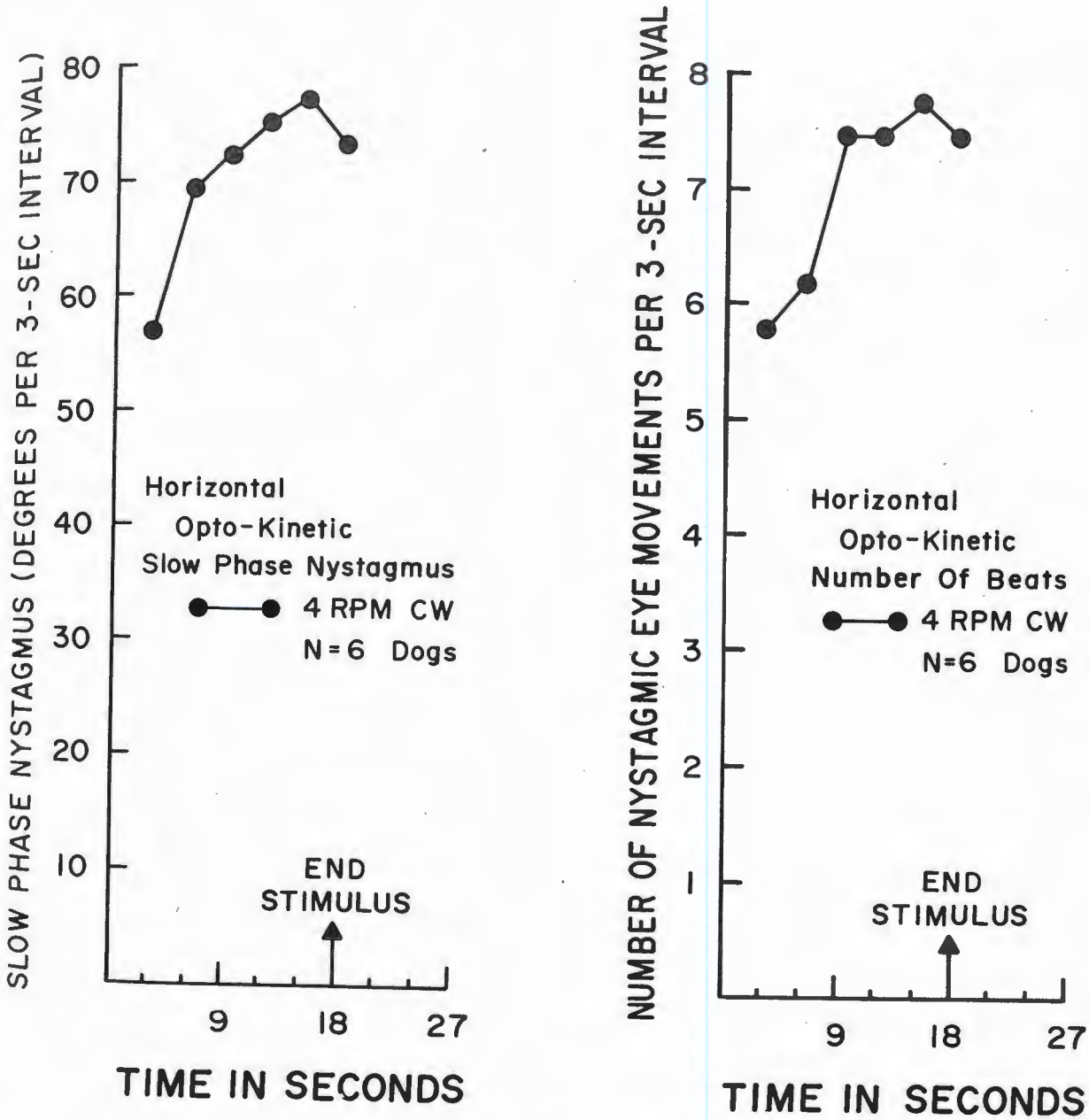


FIGURE 2. Slow-phase and frequency plots of horizontal optokinetic nystagmus for six dogs.

ures up through the first 12–18 sec of the 30-sec stimulus period. No striking difference in output between the two directions of response is evident and statistical tests (for correlated data) showed no significant directional differences in total output for either slow-phase (t=0.254) or frequency (t=1.895; t of 2.57 required for .05 level of significance).

For a better evaluation of the time-course of the optokinetic response, data obtained from seven parrots (including the six noted above) during 45-sec periods of CW drum rotation were plotted (Figure 3). It is clear that the nystagmus builds to a peak between 12–30 sec and then shows some decline. The steady build-up of the response is of considerable magnitude; for fre-

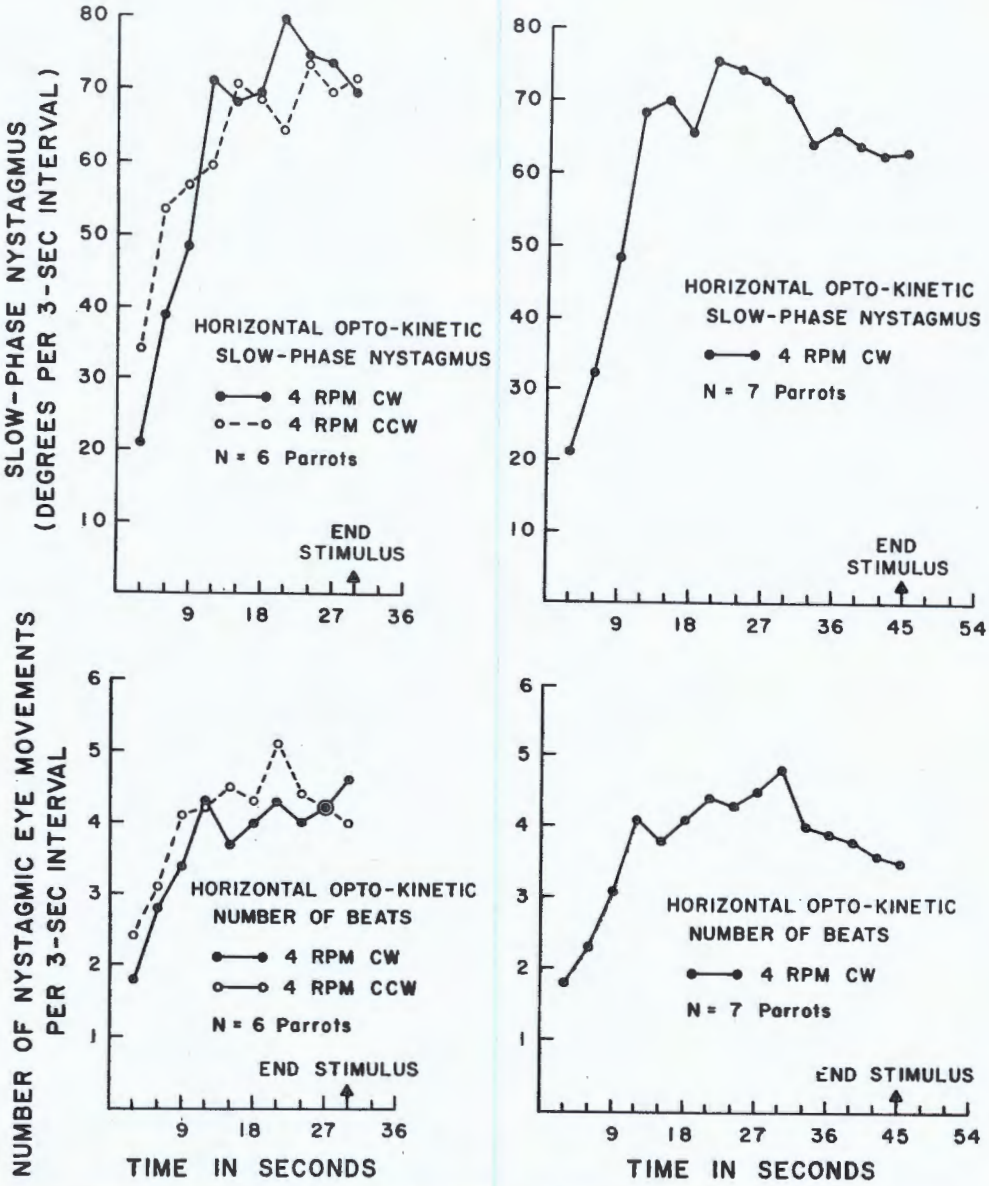


FIGURE 3. A comparison of the ocular responses of African parrots during 30 sec of CW and CCW optokinetic stimulation, and the time course of the response during 45 sec of stimulation. Note the extended period of build-up of nystagmus similar to that obtained from dogs (compare with Figure 2).

quency and for slow-phase data, the peak values are more than three and one-half times the output recorded during the first 3-sec interval. The decline, approximately 15 percent for both slow phase and frequency, may be only apparent (i.e., a random variation) and probably should be evaluated in terms of the results obtained from the cats over longer time periods.

Cats: Horizontal Nystagmus. Ten cats were exposed to 30-sec optokinetic trials with both CW and CCW drum rotation. A sample tracing appears in Figure 4, and a plot of the bidirectional comparison is in Figure 5. The latter figure and Table 1 provide three clear bits of information: (1) There is no statistically significant directional difference in magnitude of the optokinetic response; (2) The nystagmus shows a steady build-up throughout the stimulus period; (3) Following stimulus termination, the optokinetic response declines steadily and gives way to a reversed afternystagmus, i.e., to a secondary optokinetic nystagmus (in 17 of the 20 cases).

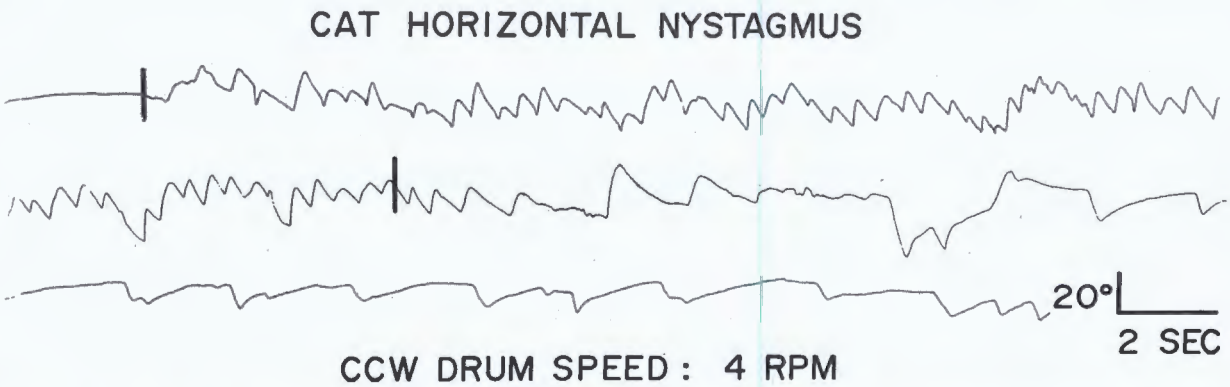


FIGURE 4. A tracing of horizontal nystagmus elicited from a cat during and following 30 sec of optokinetic stimulation. The tracing is continuous; vertical bars demarcate the stimulus period. All lights were extinguished at the moment of stimulus termination. Note the early appearance of secondary nystagmus.

With respect to the latter, there were no significant directional differences in output (Table 1).

Of 12 cats exposed to CW drum rotation for periods of 15-, 30-, 60-, and 120-sec, good records were obtained from all animals for the 60-sec stimulus, and from 11 animals each for the other stimuli. The mean slow-phase response and the mean frequency, plotted in 3-sec intervals during the stimulus period, appear in Figures 6 and 7. Peak slow-phase response appears to require at least 24 sec of stimulation, whereas average peak frequency occurs after 15–21 sec of stimulation. In any event, there is a fairly prolonged build-up period and, after reaching a peak, the nystagmus is variable but shows an inclination to decline in frequency after about one min of the 120-sec stimulus, whereas the slow-phase measures begin to decline at about that same time but recover to the original levels during the 90–120 sec phase of the stimulus. This combination of occurrences for the two response measures may indicate the influence of changes both in alertness of the animals and in their focus of gaze, as well as the possibility of some adaptation.

Afternystagmus (i.e., nystagmus recorded after stimulus termination) is plotted in Figure 8. The last nine sec of the four stimulus periods are also included for comparison purposes. Examination of these plots reveals: (1) only slight differences in the output levels during the last nine sec of the stimulus periods; (2) a trend (significant only for frequency) for the primary responses during the 15-sec stimuli to decline more slowly following stimulus termination, but this may reflect differences in output level and response tendency (build-up of nystagmus) during the last 3-sec of the stimulus more than it does an overall effect of stimulus duration; (3) the magnitude of secondary nystagmus did not appear to be influenced by stimulus duration with the exception that there was a statistically significant trend for the 15-sec stimulus (which was too short to permit primary nystagmus to reach its peak) to yield the least slow-phase secondary nystagmus; no other slow-phase comparisons produced significant differences (Table 1) and, following inspection of Figure 9, no statistical tests were conducted for the frequency data. Secondary nystagmus was present in 43 of the 45 records.

Cats: Vertical Nystagmus. Vertical optokinetic nystagmus was obtained from five cats. However, it was possible consistently to elicit a good ocular response in only one direction, i.e., with the fast-phase beating down (toward the mouth). A tracing obtained from one animal appears in Figure 9. The difference between the two directions of eye movement is striking and it occurs irrespective of the head position of the cat; whether the animal is placed on its right or its left side, drum rotation in the direction which would elicit up-beating nystagmus fails to produce a consistent response of reasonable quality in most cats, whereas good down-beating nystagmus can be fairly readily obtained.

Slow-phase and frequency measurements of down-beating vertical nystagmus were plotted for 15-sec and 60-sec stimulus durations (Figure

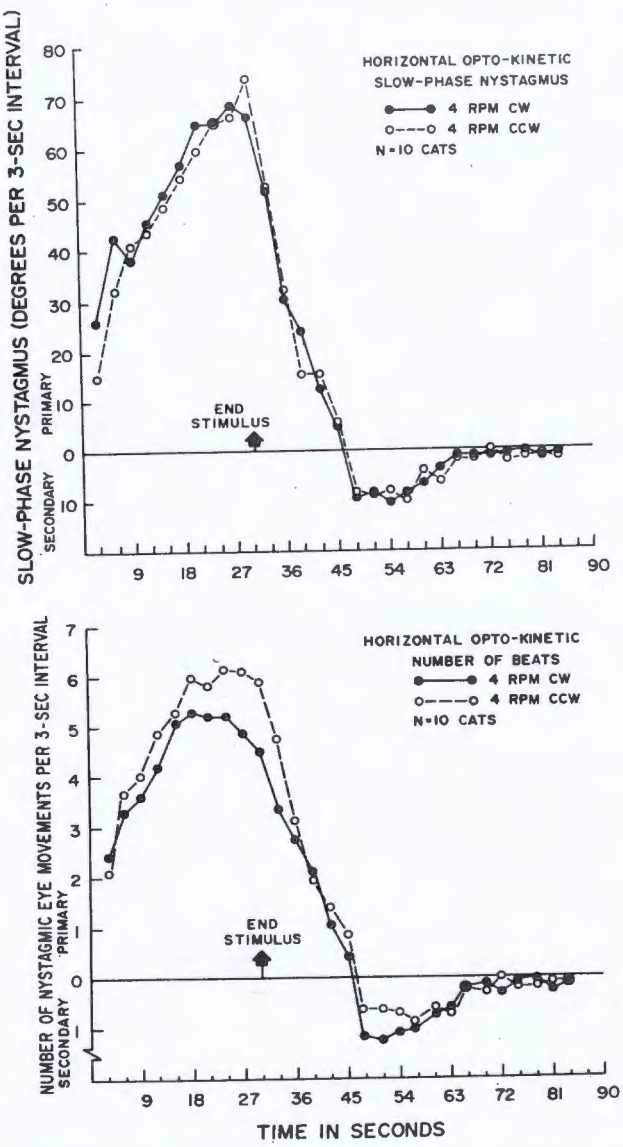


FIGURE 5. A comparison of the horizontal ocular responses of cats during and following 30 sec of CW and CCW optokinetic stimulation. All lights were extinguished at the moment of stimulus termination. The same build-up of nystagmus occurs as found in the data from parrots and dogs (compare with Figures 2 and 3).

10). The response curves show some irregularity but give evidence of a build-up period and the possibility of a decline; however, the peak of the response does not occur until after about 45 sec of stimulation. Weak secondary nystagmus was observed on only one of the 10 possible occasions (following the 60-sec stimulus).

Human Subjects: Horizontal Nystagmus. Human subjects showed no significant directional differences in nystagmic output to 30-sec periods of CW and CCW drum rotation (Table 2) nor were any clear secondary optokinetic responses evident (Figure 11). With respect to the latter, only five (three CW and two CCW) of the total of 20 trials showed even slight evidence of secondary responses; these occurrences were spread among four subjects and were of such small magnitude that they were not plotted. There were no differences referable to sex or to handedness.

Plots depicting responses during the 15-, 30-, 60-, and 120-sec stimuli were quite regular in appearance and showed neither a build-up period nor a declining response during stimulation (Figure 12 and 13) with one exception; there may be a tendency for the frequency of the eye movements to be slightly higher during the first two or three 3-sec intervals of a given stimulus. In examining afternystagmus (Figure 14), the last nine sec of the average responses during each of the four stimulus periods were also plotted; no differences attributable to the stimulus durations are evident. However, there was a significant tendency for afternystagmus to be of greater magnitude following the longer stimulus durations (Table 2). The 15- and the 30-sec stimuli produced significantly less afternystagmus than either the 60- or 120-sec stimuli; no other comparisons showed statistical significance. Secondary nystagmus was again weak, and was scored (but not plotted) as possibly present during only seven of the 40 trials; three of these were following the 15-sec stimulus, two after the 30-sec stimulus, and two following 120 sec of optokinetic stimulation.

Human Subjects: Vertical Nystagmus. Unlike the cats, human subjects gave consistent vertical nystagmus to both directions of drum rotation. There was no statistically significant difference between output levels (Table 2) for the two directions (Figure 15). Secondary nystagmus was not obtained. Following the 30-sec stimuli, down-beating nystagmus was of considerably longer duration than the up-beating response, but this was attributable to two subjects.

In plotting the time course of the vertical responses during the four stimulus periods, neither slow-phase (Figure 16) nor frequency (Figure 17) demonstrated a build-up or a decline, with the same exception noted for the frequency of

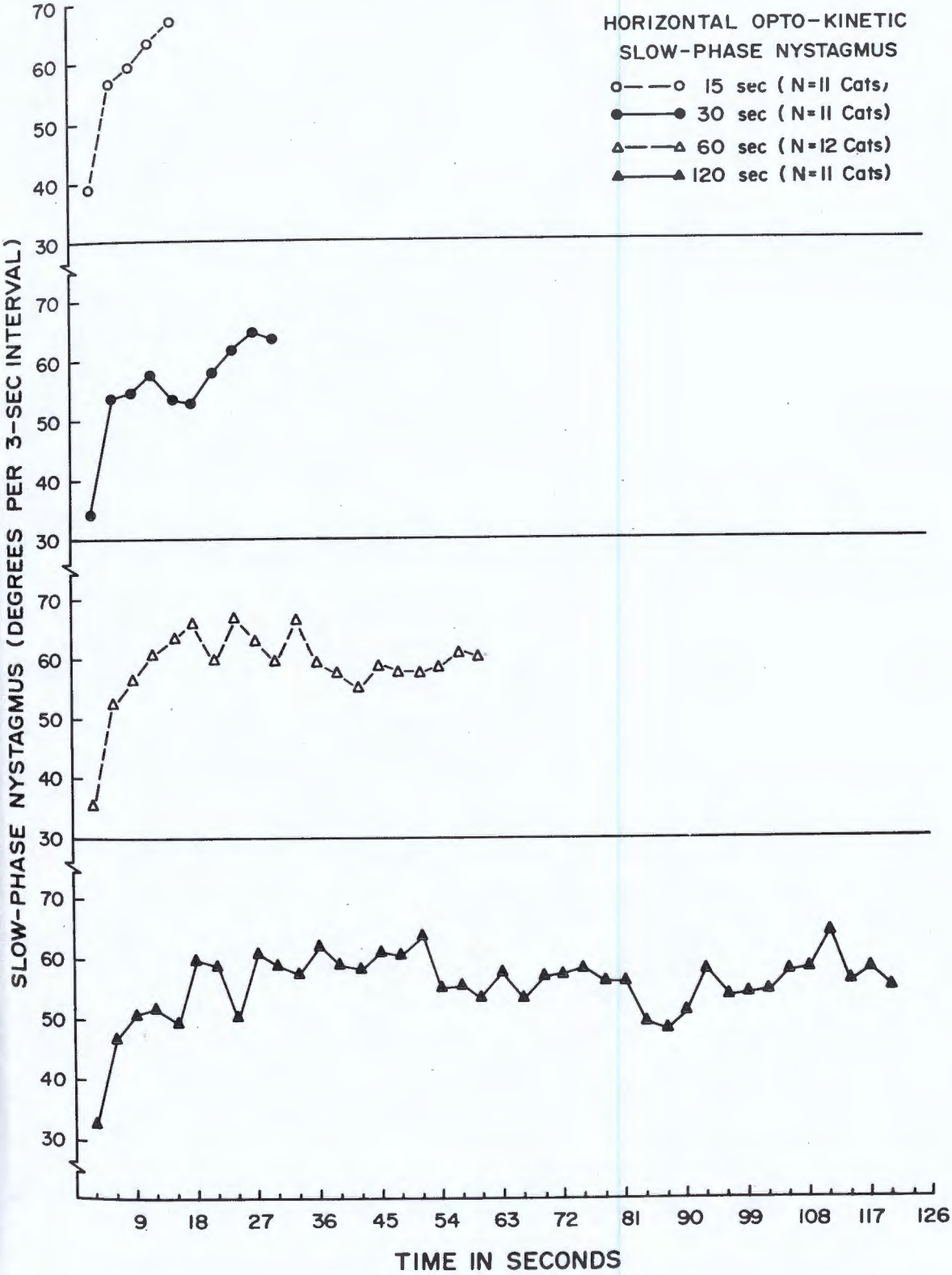


FIGURE 6. Horizontal slow-phase responses from cats during four stimulus durations. A build-up period, some variability, but no clear evidence of adaptation are evident. Drum rotation was 24°/sec.

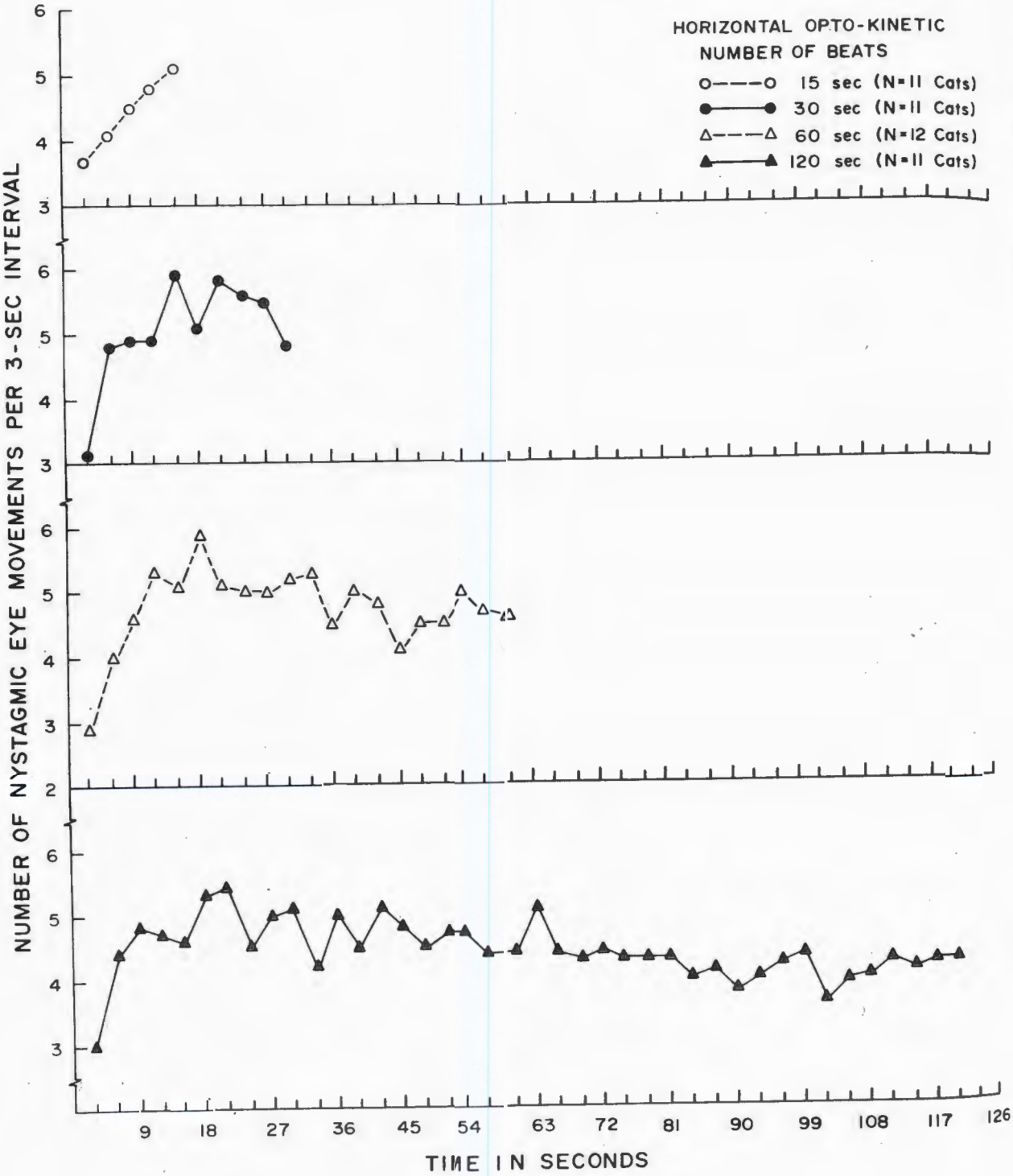


FIGURE 7. Frequency of horizontal nystagmus from cats during four stimulus durations. A build-up period is evident and some adaptation appears to occur during the 2-min stimulus.

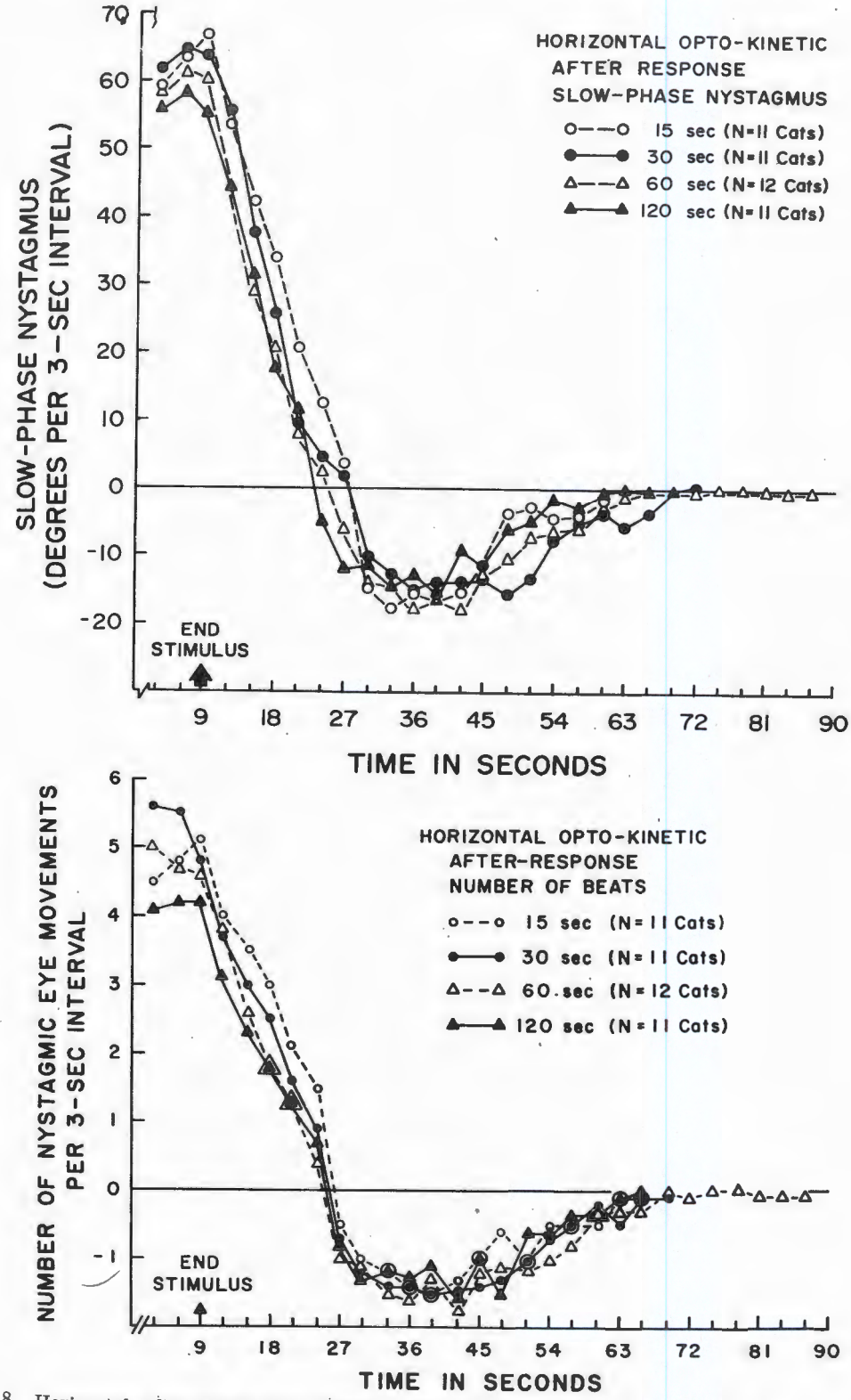


FIGURE 8. Horizontal afternystagmus (primary and secondary) from cats following the four durations of stimulation. The last nine sec of response during each stimulus are included. All lights were extinguished at the moment of stimulus termination. The small differences in output among conditions during the last nine sec of stimulation may reflect a slight adaptation effect.

TABLE 1

Results of statistical comparisons between correlated optokinetic nystagmus scores for cats. Ten animals were used in each comparison.

	Comparison	Measure	t	Level of Significance
Horizontal Output Primary	CW vs. CCW (30-sec stimulus)	Slow-phase	0.011	---
		Frequency	1.939	---
Horizontal Output Secondary	CW vs. CCW (30-sec stimulus)	Slow-phase	0.028	---
		Frequency	1.083	---
Horizontal Primary Afternystagmus	15 vs. 30 sec	Slow-phase	2.893	.02
		Frequency	2.049	---
	15 vs. 60 sec	Slow-phase	3.173	.02
		Frequency	3.199	.02
	15 vs. 120 sec	Slow-phase	1.758	---
		Frequency	2.354	.05
	30 vs. 60 sec	Slow-phase	2.524	.05
		Frequency	2.009	---
	30 vs. 120 sec	Slow-phase	0.159	---
		Frequency	0.971	---
	60 vs. 120 sec	Slow-phase	0.215	---
		Frequency	0.597	---
Horizontal Secondary Nystagmus	15 vs. 30 sec	Slow-phase	3.359	.01
	15 vs. 60 sec	Slow-phase	3.674	.01
	15 vs. 120 sec	Slow-phase	3.144	.02
	30 vs. 60 sec	Slow-phase	0.818	---
	30 vs. 120 sec	Slow-phase	0.495	---
	60 vs. 120 sec	Slow-phase	0.173	---

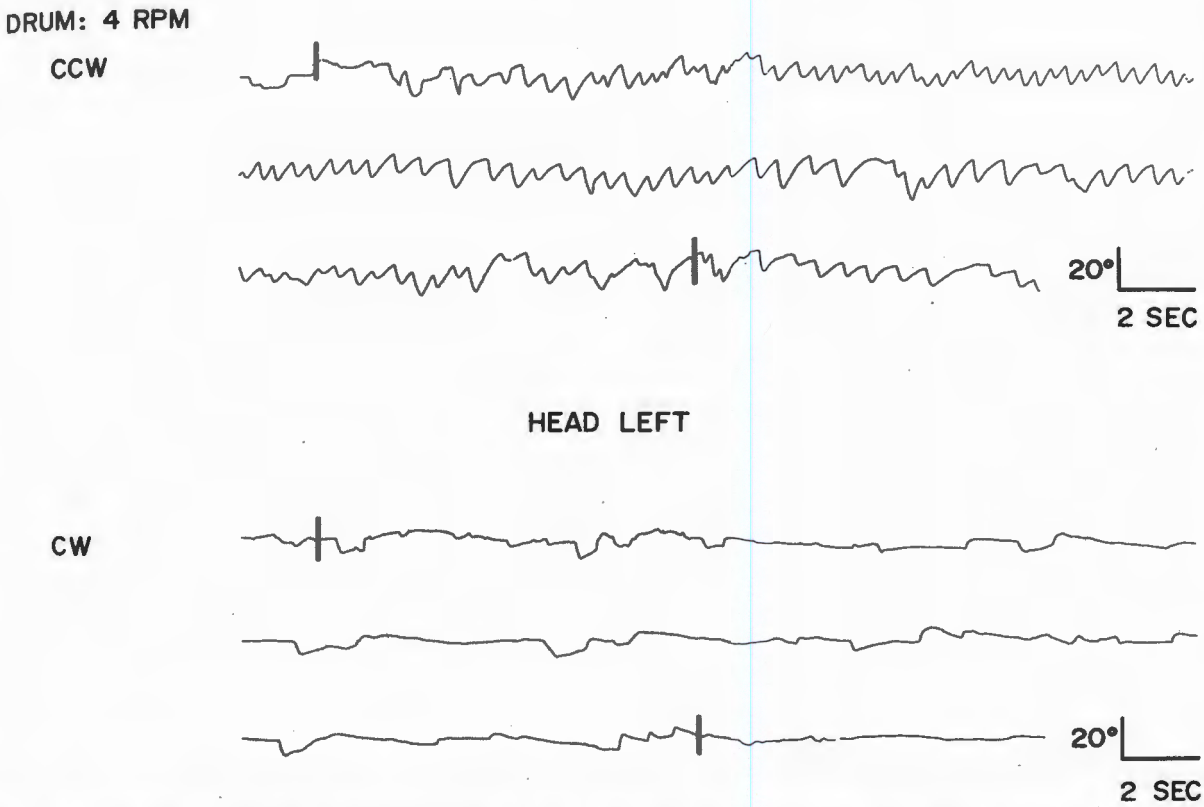


FIGURE 9. Tracings of vertical nystagmus from a cat. Vertical bars demarcate the 60-sec stimulus. All lights were extinguished at the moment of stimulus termination. Up-beating nystagmus could not be elicited for sustained periods from most of the animals tested. Note the poor quality of the response during the first few sec.

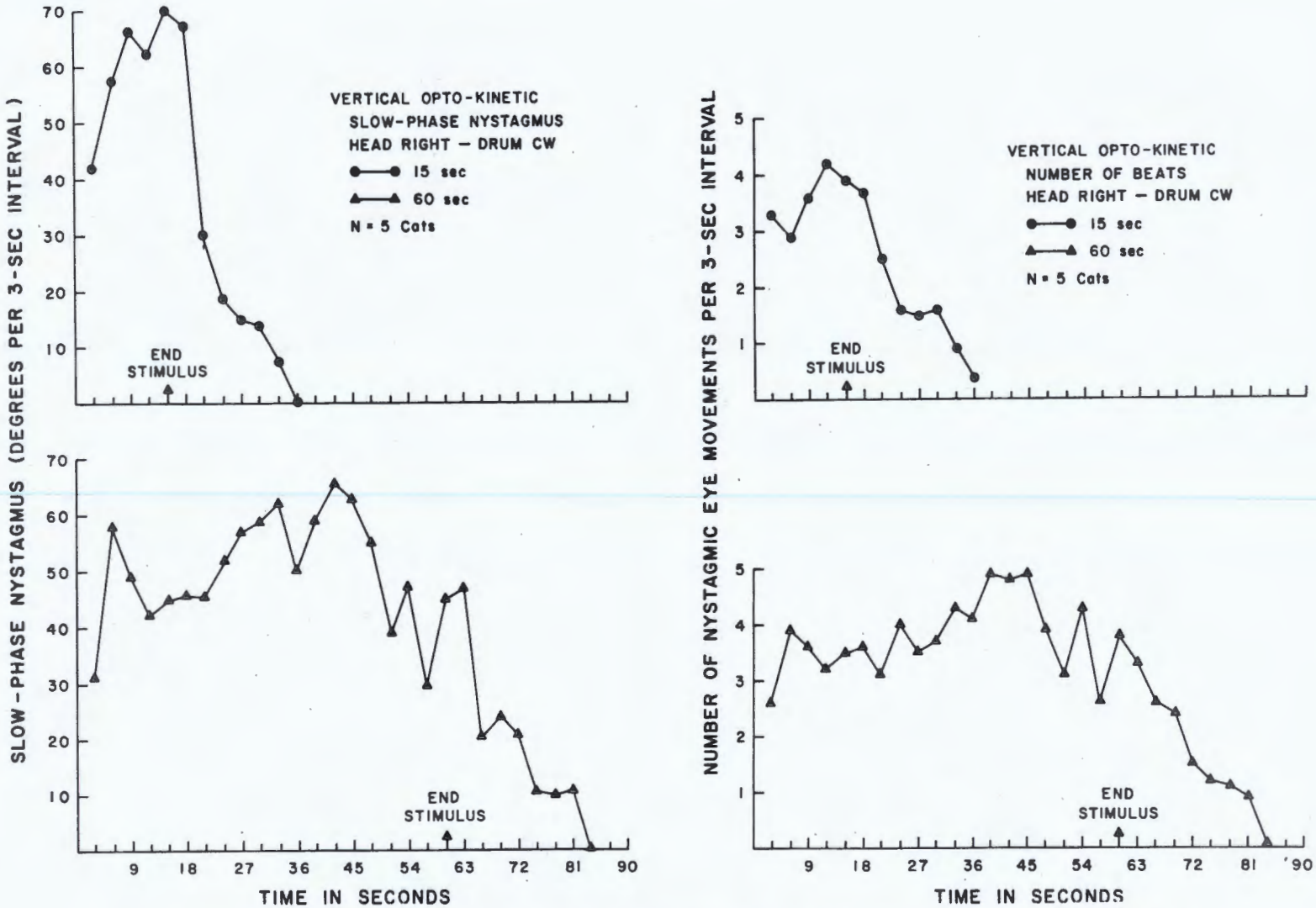


FIGURE 10. Vertical ocular responses from cats to two durations of 24°/sec stimulation. The response is more variable than that obtained for horizontal nystagmus, but appears to evidence a build-up period. All lights were extinguished at the moment of stimulus termination.

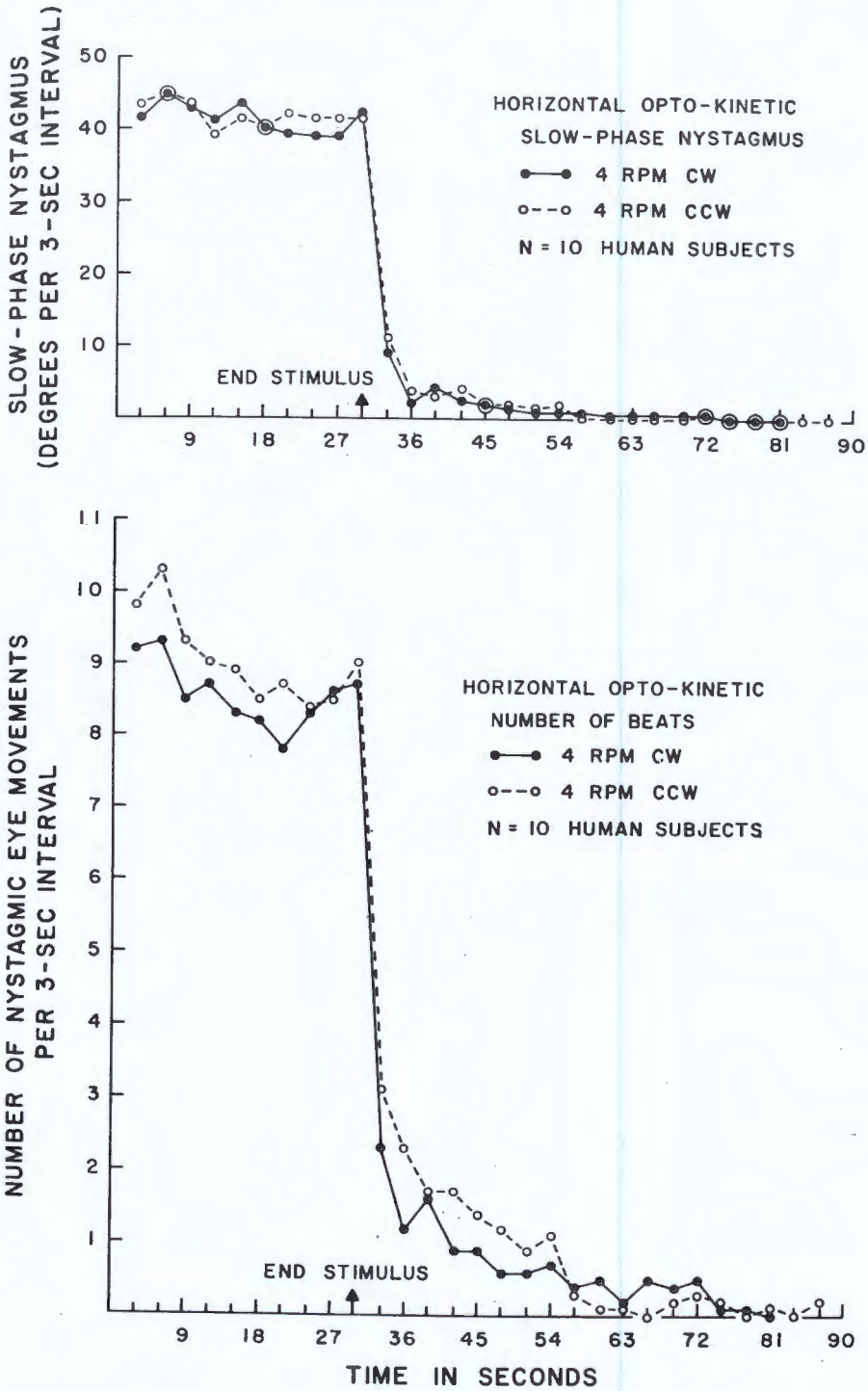


FIGURE 11. A comparison of the horizontal ocular responses of human subjects during and following 30 sec of 24°/sec CW and CCW optokinetic stimulation. Note the sharp drop in output following stimulus termination at which moment all lights were extinguished.

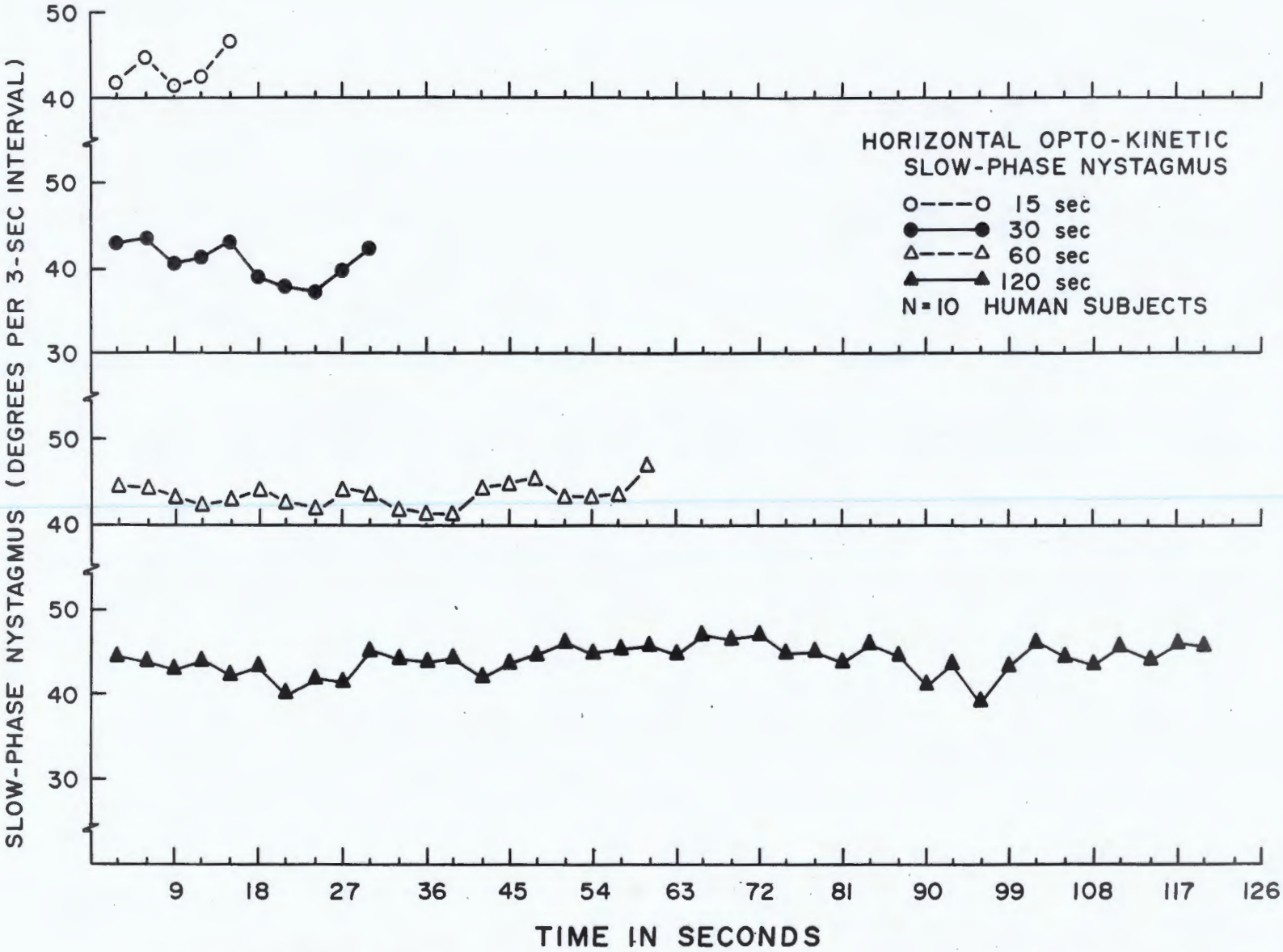


FIGURE 12. Horizontal slow-phase responses from human subjects during four stimulus durations. The nystagmus is relatively constant even during the 2-min stimulus. Drum speed was 24°/sec.

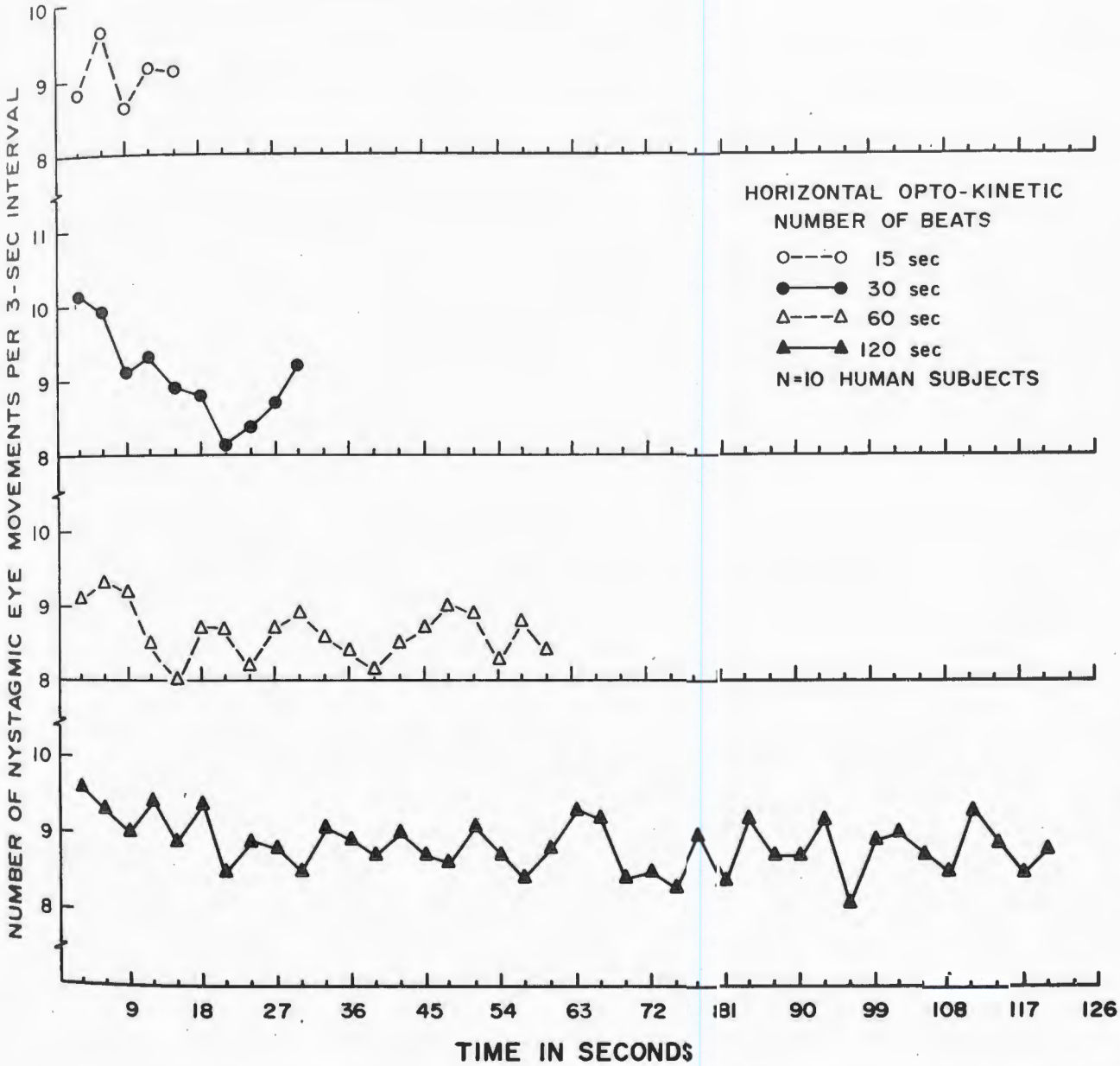
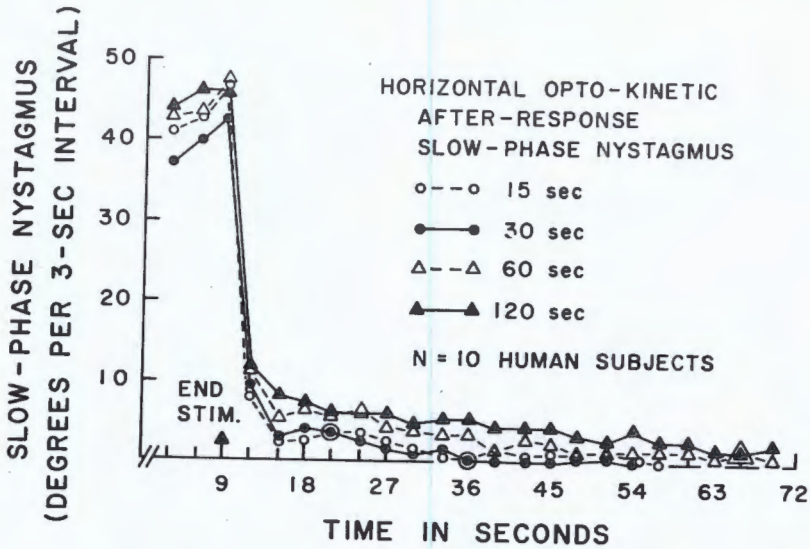


FIGURE 13. Frequency of horizontal nystagmus from human subjects during four durations of 24°/sec stimulation.



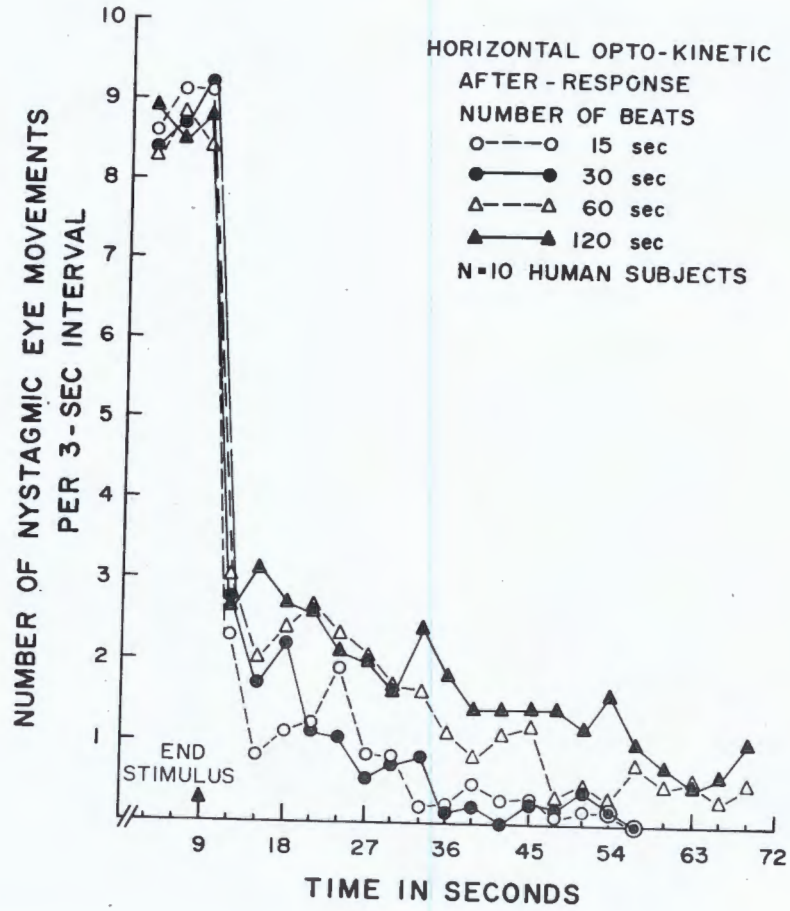


FIGURE 14. Horizontal afternystagmus from human subjects following the four durations of stimulation; the last nine sec of response during each stimulus are included. The output of nystagmus drops sharply following stimulus termination (when all lights were extinguished) and the amount of afternystagmus appears related to the duration of optokinetic stimulation.

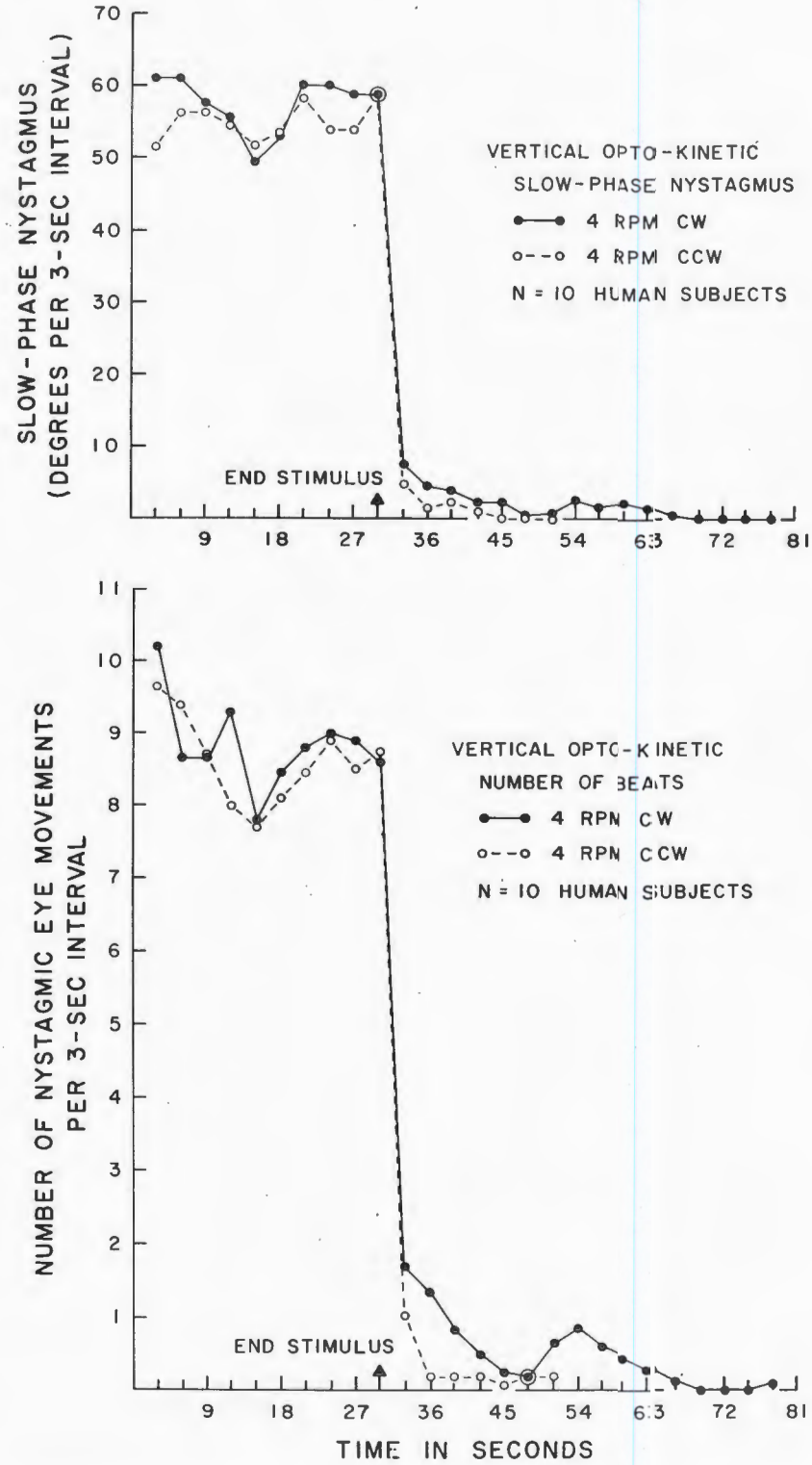


FIGURE 15. A comparison of the vertical ocular responses of human subjects during and following 30 sec of CW and CCW optokinetic stimulation. Note the sharp drop in output, similar to that obtained for horizontal nystagmus, following stimulus termination (at which moment all lights were extinguished). The longer response following CW stimulation is due to two subjects and, primarily, to only one of them.

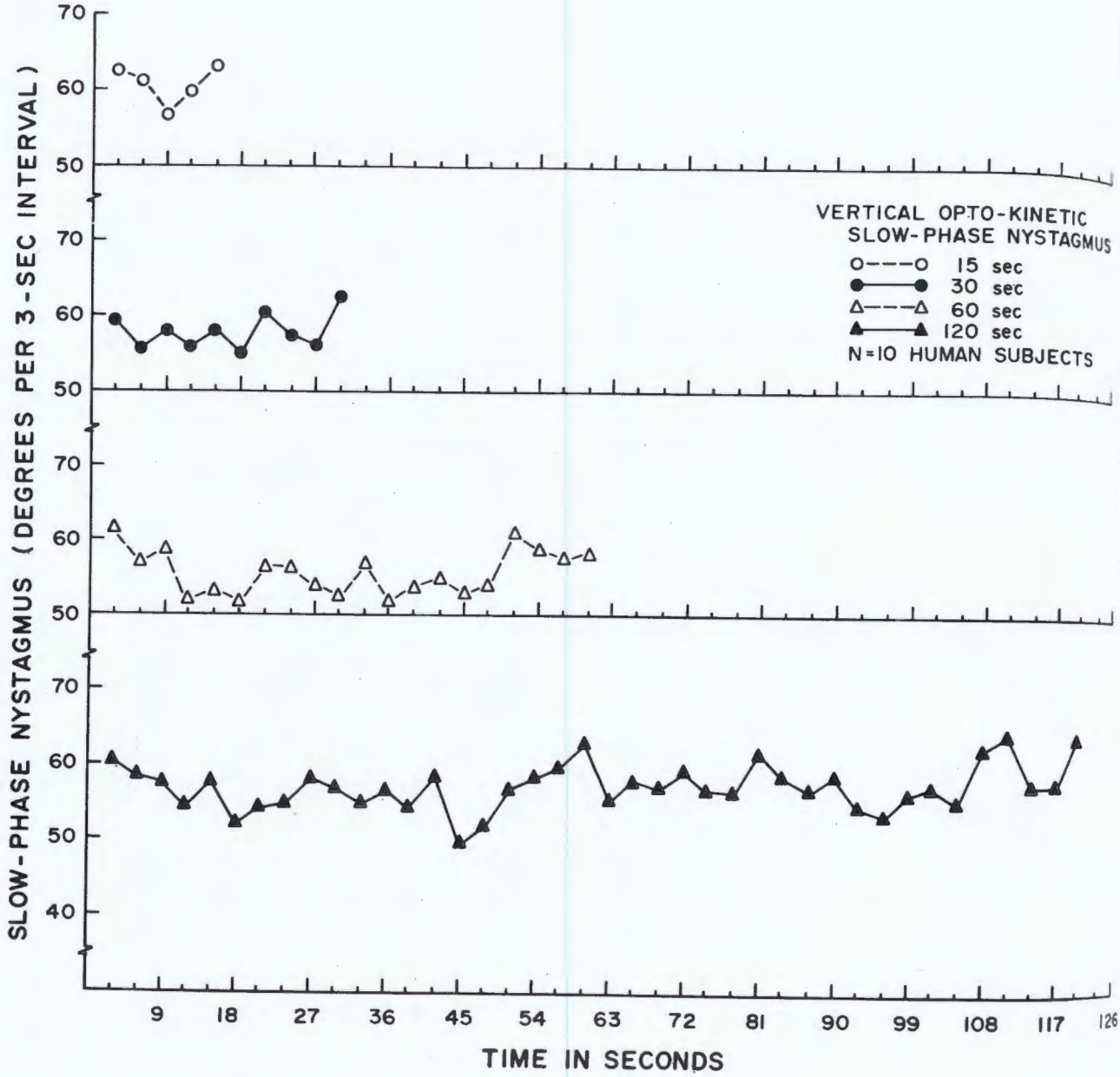


FIGURE 16. Vertical slow-phase responses from human subjects during four stimulus durations. No adaptation effects are apparent. Drum speed was 24°/sec.

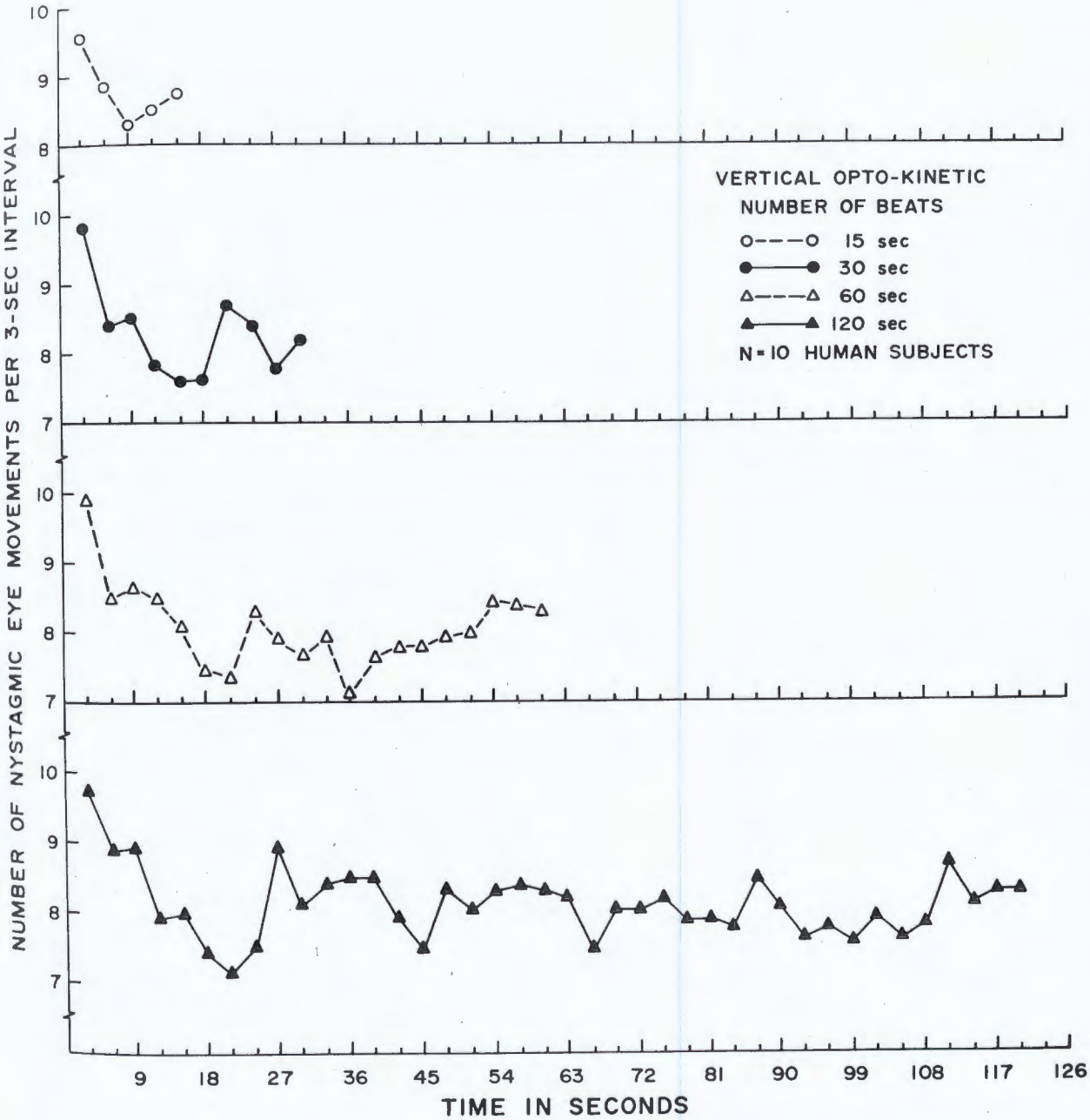
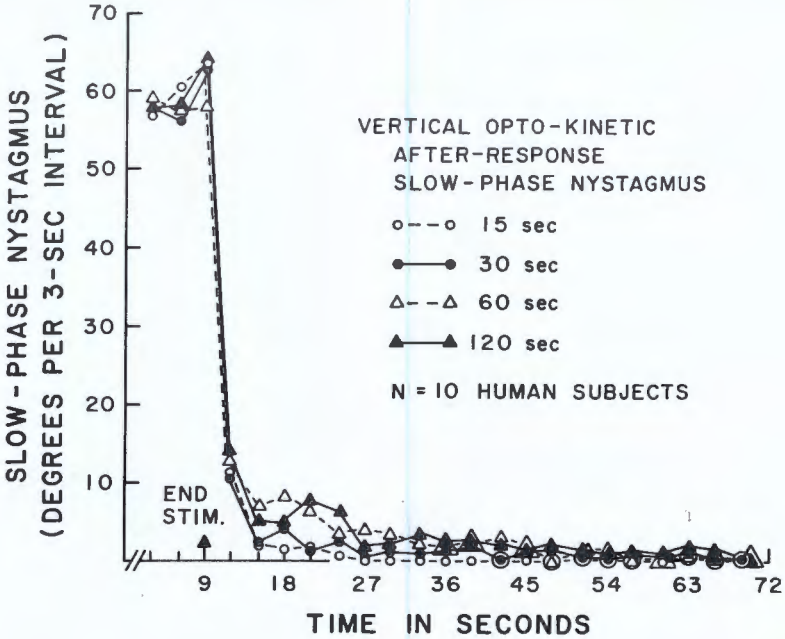


FIGURE 17. Frequency of vertical nystagmus from human subjects during four durations of 24°/sec stimulation. More eye movements appear to occur in the first few seconds of stimulation, but no clear adaptation effects are apparent.



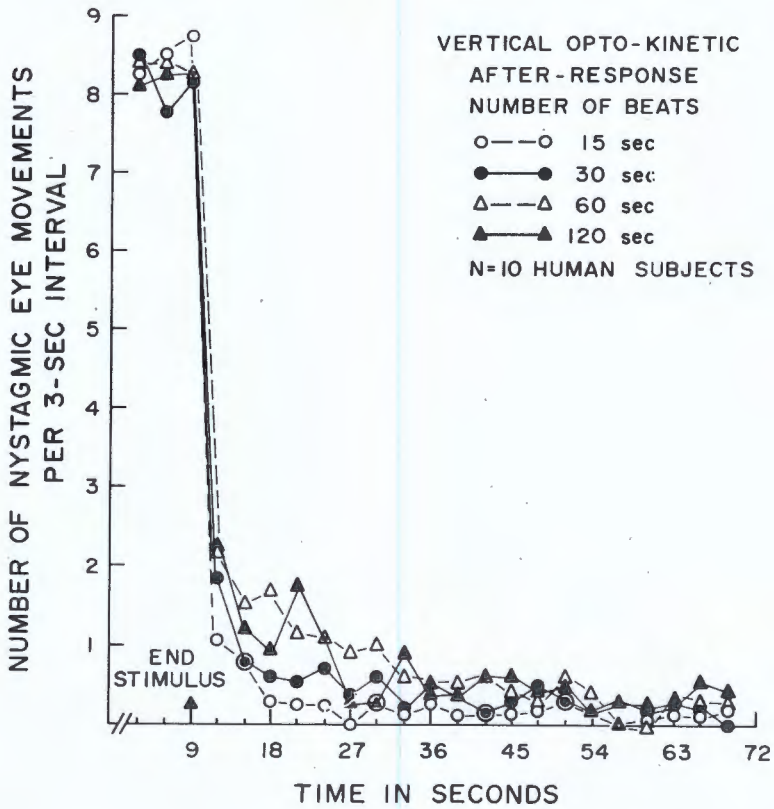


FIGURE 18. Vertical afternystagmus from human subjects following the four durations of stimulation; the last nine sec of response during each stimulus are included. The output of nystagmus drops sharply (as did the horizontal response) following stimulus termination (when all lights were extinguished). Although there appears to be a tendency for the amount of afternystagmus to be greater following longer stimulus duration, no consistent statistical relationships were obtained.

the horizontal optokinetic response, i.e., the frequency of eye movements tended to be higher for the first two or three intervals during each stimulus.

As was the case with horizontal responses, combined plots of the final nine sec of the four stimulus durations showed no effect of duration on output levels (Figure 18). Afternystagmus again showed a tendency toward greater output following the longer stimulus durations, but the only statistically significant differences were between the 30- and 60-sec outputs (Table 2). Secondary nystagmus was weak, if it occurred at all, and may have been present during only four of the 40 trials; two of these were following the 15-sec stimulus, and one each following the 60-sec and 120-sec stimuli.

IV. Discussion.

Animals. For the birds and the cats examined here, it is clear that: (a) there are no directional differences in output of horizontal optokinetic nystagmus; (b) the optokinetic response builds up throughout the initial 20–30 sec before reaching a relatively stable output level. The latter point also appears to be true for dogs.

The fact that the velocity of the slow-phase takes some time to reach a maximum value was noted by ter Braak[2] in studies of rabbits. He attributed this to "central resistance" and compared it with mechanical friction (inertia). Whatever the cause, it is clear that, during the initial seconds of stimulation, horizontal optokinetic nystagmus is not well developed (see Figure 4), i.e., the rhythmic pattern is not established. Then for another period of several seconds, while the eye movements are rhythmical, the slow-phase displacement (or velocity) of the eye continues to increase until it finally levels off and remains relatively constant. The relationship of the maximum eye velocity to the velocity of stimuli cannot be ascertained by the data presented here; the calibration factors were based upon the response to an arbitrarily selected portion of the stimulus period. However, ter Braak[2] indicated that (with a freely movable eye), the (optimal) speed of the slow-phase is generally a little less than that of the stimulus since the stimuli would no longer be effective if eye velocity and stimulus velocity were the same. However, under special conditions, eye speed may exceed stimulus speed.[2] It is possible that the build-up period and those periods during which eye velocity exceeds stimulus velocity are important for the animal in gaining information about the speed of movement of objects in the visual field, i.e., that those periods provide error signals which give the animal an accurate ("test") basis for judging the speed of object movement.

These results point to a clear methodological caution in using optokinetic data from animals to provide calibration factors for other measures of eye movement (e.g., vestibular nystagmus), viz., the data used to derive the calibration factor must be from the relatively stable period of the response (i.e., after at least the initial 10 sec of stimulation). If other time periods are used or are selected arbitrarily, (a) comparisons from trial-to-trial or day-to-day will be made on inaccurate basis, and (b) the converted measurements will not reflect the true amount of eye movement. Other data[20] provide an additional caution; the relationship between eye velocity and stimulus velocity is "not an unitary linear" one in the cat.

Upon termination of stimulation, in darkness, responses of the cat (and of rabbits[2]) decay gradually (primary afternystagmus). ter Braak attributed this characteristic of the optokinetic response to the same "central resistance" or inertia that he used to account for the build-up of nystagmus during the initial seconds of stimulation. In the cat (and in rabbits, at least after prolonged optokinetic stimulation[28]) the afternystagmus then gives way to a secondary (reversed) ocular nystagmus. These secondary data from the cat are strikingly reminiscent of the characteristics of the vestibular eye-movement response following termination of an angular acceleration. As noted by Wolfe,[32] the strong secondary nystagmus so readily obtained following vestibular stimulation of the cat may be more closely related to the activity of the optomotor rather than the vestibular system. The results are also pertinent to the "reflex rebound" of optokinetic nystagmus (enhanced output to a change in the direction of drum rotation following 15–60 min of stimulation) and some apparent habituation reported for turtles by Hayes, Hogberg, and Hertzler.[16]

Of interest is the fact that neither the frequency nor the amount of horizontal slow-phase eye movement during the secondary phase was consistently related to the duration of the stim-

TABLE 2

Results of statistical comparisons between correlated optokinetic nystagmus scores for human subjects (N = 10).

	Comparison	Measure	t	Level of Significance
Horizontal Output	CW vs. CCW (30-sec stimulus)	Slow-phase	0.354	---
		Frequency	1.567	---
Horizontal Afternystagmus	15 vs. 30 sec	Slow-phase	0.139	---
		Frequency	0.908	---
	15 vs. 60 sec	Slow-phase	3.021	.02
		Frequency	3.547	.01
	15 vs. 120 sec	Slow-phase	2.981	.02
		Frequency	3.050	.02
	30 vs. 60 sec	Slow-phase	2.975	.02
		Frequency	2.909	.02
	30 vs. 120 sec	Slow-phase	3.024	.02
		Frequency	2.871	.02
	60 vs. 120 sec	Slow-phase	2.159	---
		Frequency	1.784	---
Vertical Output	CW vs. CCW (30-sec stimulus)	Slow-phase	1.483	---
		Frequency	1.274	---
Vertical Afternystagmus	15 vs. 30 sec	Slow-phase	1.272	---
		Frequency	1.377	---
	15 vs. 60 sec	Slow-phase	2.213	---
		Frequency	2.113	---
	15 vs. 120 sec	Slow-phase	1.824	---
		Frequency	1.925	---
	30 vs. 60 sec	Slow-phase	2.775	.05
		Frequency	2.345	.05
	30 vs. 120 sec	Slow-phase	2.047	---
		Frequency	1.671	---
	60 vs.120 sec	Slow-phase	0.016	---
		Frequency	0.250	---

alus within the 15–120 sec intervals used here. The significantly lower slow-phase secondary output for the 15-sec stimulus probably can be attributed to the fact that the peak output level for the primary nystagmus had not been reached before the stimulus was terminated.

Vertical optokinetic responses from the cat also showed evidence of a build-up period and a gradual decay after stimulus termination. However, it was more difficult to determine the time-course characteristics of the vertical eye movements; they were less regular than horizontal nystagmus and were obtained with the animals in an undesirable position (on their sides). It is possible that the vertical response builds up throughout the initial 45 sec of optokinetic stimulation and then begins to decay (adaptation) during further periods of stimulation. Of more interest, however, was the inability consistently to evoke an up-beating nystagmus from the cats; only down-beating (i.e., toward the mouth) eye movements could be uniformly elicited regardless of which eye was used for recording, or upon which side the animal was placed, or in which direction the drum was turned. We have no explanation for this directional difference although Krieger and Bender[22] reported that vertical optokinetic reactions from monkeys were "less apparent" when the fast phase beat from head to foot (downward). This latter finding is the opposite of what we have observed in cats; to make certain of our findings, we have supplemented our electronystagmographic recordings with direct visual observation both in this study and in an earlier one[8] in which the same results were obtained from a group of 16 cats. Asymmetries in vertical nystagmus have also been reported for humans.

Humans. Like the animals, human subjects showed no significant difference between right-beating and left-beating horizontal nystagmus and there was no significant adaptation apparent for responses lasting as long as two min. These findings do not agree with those reported by Wolfe.[32] We have no explanation for the lack of directional preponderance found here and the marked slow-phase asymmetry (approximately 40 per cent more displacement during CW as compared with CCW drum rotation) noted by Wolfe, other than possible chance differences among the subject populations used. Other studies,[e.g., 8 13 23 25] also have not found consistent directional differences among humans. The apparent "marked adaptation" shown by Wolfe's subjects (a steady slow-phase decline from the first five sec period of stimulation through the 25–30 sec period, comprising a reduction of approximately 20–25 per cent) is probably due to alertness factors and changes in gaze. Characteristics of optokinetic nystagmus are known to be affected by the method of gaze used by the observer, e.g., "look" vs. "stare" nystagmus.[2 19] However, our experience indicates that even though active tracking of a stripe ("look" nystagmus) may not occur, there is a tendency over time for the focus of gaze to change, i.e., the plane of visual fixation appears to shift. When subjects are instructed to maintain their gaze in the "plane" of the black stripes (the white background is frequently perceived as more distant in our device), and are encouraged to maintain a state of alertness, no "adaptation" occurs, at least for the periods of stimulation used here. Figure 19 depicts tracings obtained under instructions to be alert (supplemented by verbal encouragement during the trial) and instructions to relax while staring in the plane of the black stripes. Similar results have been reported in recording vestibular nystagmus,[5 6] as well as vertical optokinetic responses.[29] Moreover, Mackensen[24] has noted that, during the course of six min of optokinetic stimulation, the amplitude of nystagmus increases (particularly after two min) to a marked degree while frequency declines only slightly.

Unlike the animals, there were obtained from the human subjects (a) no statistically significant directional differences in the overall output of vertical nystagmus, (b) no build-up period for slow-phase nystagmus to reach its maximal level, (c) a sharp drop in nystagmic output (in darkness) following stimulus termination, (d) a prolonged primary afternystagmus which was of greater magnitude following longer durations of optokinetic stimulation, (e) almost no secondary nystagmus, (f) a tendency for both horizontal and (particularly) vertical nystagmus to show a higher frequency of eye movements during the first few sec of stimulation. Several of these findings require comment.

Although there were no significant group differences between up-beating and down-beating vertical nystagmus, there were several striking directional differences for individual subjects

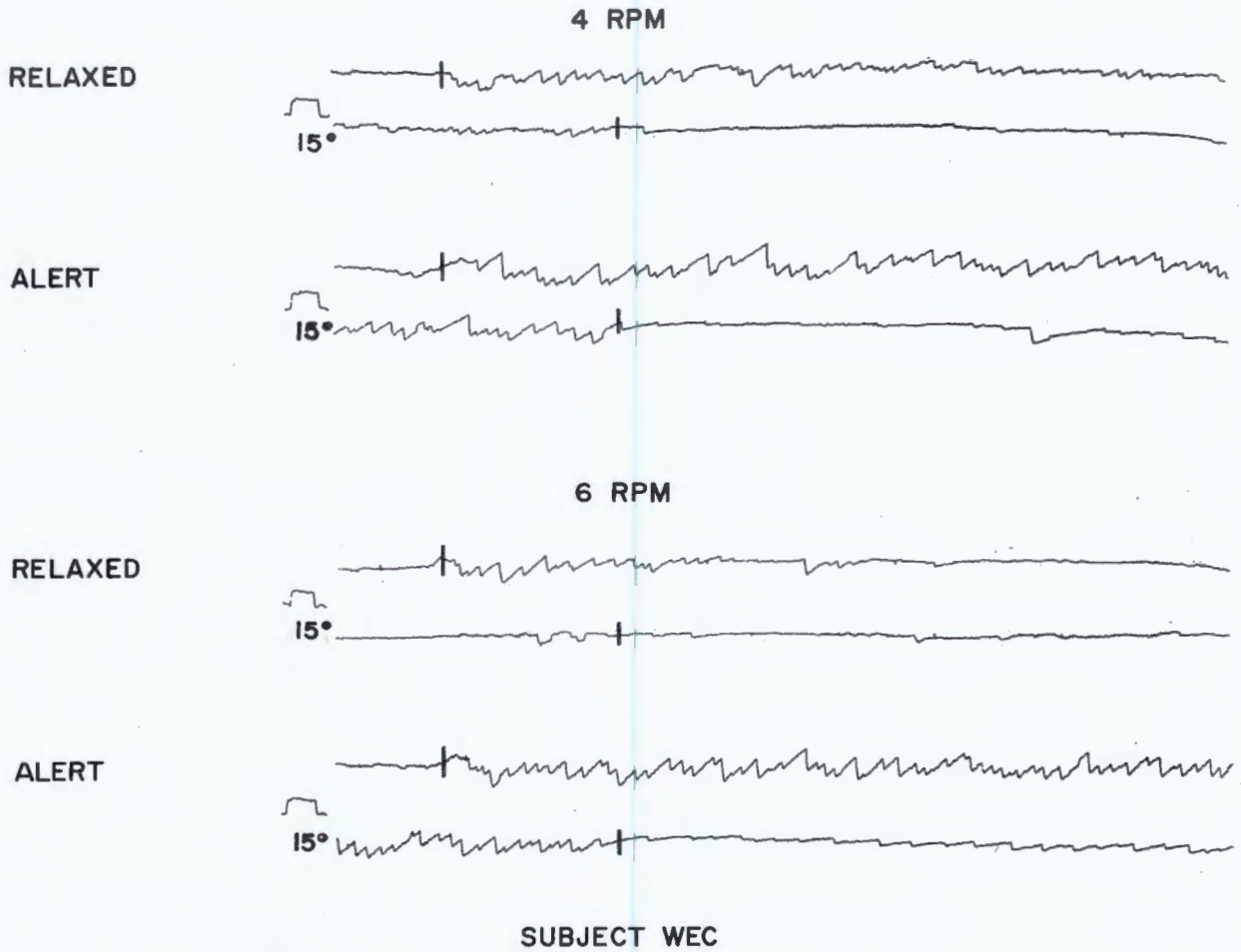


FIGURE 19. Tracings of horizontal nystagmus from a human subject given instructions to focus in the plane of the black stripes and either to (a) maintain alertness (verbal encouragement was also given on these "alert" trials) or (b) relax but maintain focus. CW stimuli were 30 sec in duration (demarcated by the vertical bars) and all lights were extinguished at the moment of stimulus termination. Clear "adaptation" is evident during the 4 rpm stimulus under the relaxed condition; the alert condition yielded brisk responses to both stimulus rates.

(Figure 20). A marked asymmetry in vertical responses from humans has been noted before;[29] in one sample of 20 subjects, the frequency of eye movements tended to be higher more often in the up-beating direction. In our sample, six of the 10 subjects showed an up-beating preponderance, but three of these differed directionally by less than 10 per cent; of the four subjects who had higher-frequency nystagmus in the down-beating direction, only two had directional differences exceeding 10 per cent. It is clear that, in at least some apparently normal subjects, a marked directional difference in frequency of vertical optokinetic nystagmus may occur. Directional differences in vertical nystagmus of vestibular origin appear in the observation by Hixson and Niven[18] that a vestibular stimulus which induces vertical nystagmus with fast-phase down causes blurring (loss of visual acuity) for longer periods than an equivalent vestibular stimulus which produces vertical eye movements with fast-phase up. Similarly, Guedry and Benson[15] noted higher-frequency vestibular nystagmus in a down-beating direction in darkness; introduction of a visual task during a vertical vestibular nystagmus did not affect the frequency of down-beating nystagmus, but it clearly reduced the frequency of up-beating nystagmus.

The failure to obtain clear secondary nystagmus may be partly a function of the stimulus durations used in this study. Mackensen[24] reported that "in a number of healthy persons"

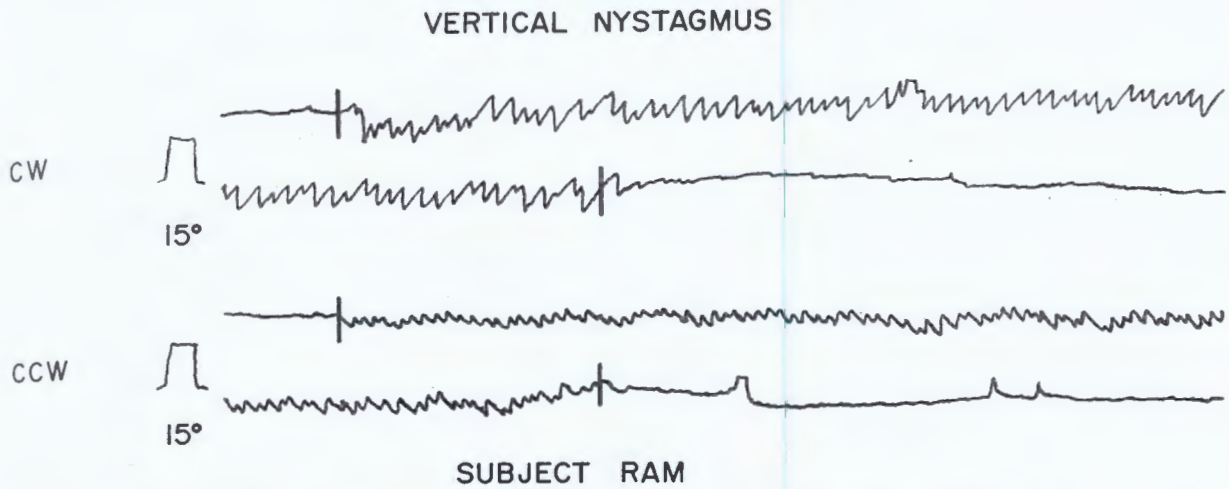


FIGURE 20. Tracings of vertical nystagmus from a human subject. Vertical bars demarcate the 30-sec periods of 24°/sec stimulation. The subject was positioned with her head tilted 90° to the right. A clear asymmetry between the characteristics of the up-beating and down-beating responses is evident. Two additional subjects showed these same marked differences, while two others demonstrated them in the opposite direction.

a secondary nystagmus was elicited following six min of optokinetic stimulation. Other investigators[27] obtained secondary optokinetic nystagmus from all four of their subjects, but their test technique was different; they used a constant angular acceleration of their drum (rather than a constant velocity) and applied a 1°/sec² stimulus for two min (the final speed of the drum was thus 120°/sec). In any event, the secondary response is not as characteristic a feature of human optokinetic reactions as it is of cats. Further, human secondary nystagmus appears to be more readily elicitable following angular acceleration than it does following periods of (constant) optokinetic stimulation of "reasonable" duration (up to two min).

A final point concerns the relationship of eye velocity to stimulus velocity. Wendt[31] presented data (obtained during harmonic rotatory stimulation of human subjects with vision permitted) which indicated that optokinetic eye speed was about 80 per cent of stimulus speed. Our vertical eye movement data agree with this figure, but our horizontal eye-movements were only about 60 per cent of stimulus speed. It is conceivable that the characteristics of the stimulus field (e.g., spacing of stimuli and type of moving stimulus) as well as stimulus speed may have a significant effect on the eye velocity. There are other possibilities. Calibration techniques which involve sweeping the eyes between two markers are reported to produce different calibration factors with changes in the distance between the subject and the markers (apparently due to accommodation-convergence differences), even though the visual angle is the same.[14] This might have affected the horizontal nystagmus data of the present study since the electrodes were at the outer canthi of the two eyes; it is less likely to have affected the vertical nystagmus data where recordings were obtained from only one eye. In addition, the scoring technique used in this study ignored (for practical purposes) the time segments taken up by the fast phases of the nystagmic movements; this approach would produce some underestimation of the slow-phase velocity.

V. Summary.

Optokinetic stimulation of dogs, parrots, and cats showed that both slow-phase displacement and frequency of eye movements increased during the initial 18 sec or more of stimulation before leveling off. There was no significant difference between right-beating and left-beating responses. Cats were studied more extensively and showed no clear adaptation effects for stimuli up to two min in duration. Cats also displayed a smoothly declining afternystagmus (in the dark) following stimulus termination; this response consistently gave way to a secondary nystagmus, the magnitude of which did not seem

to be affected by the longer stimulus durations. Vertical nystagmus from cats was less regular and could be obtained consistently only in a down-beating direction. Human subjects showed no consistent directional differences in either horizontal or vertical optokinetic nystagmus but differed from the cats in that no build-up period was evident, a sharp drop in nystagmus followed stimulus termination, the output of afternystagmus tended to be greater following longer durations of stimulation, and secondary responses were both infrequent and weak. Some striking but apparently normal asymmetries in the vertical responses of humans were noted.

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