AM 68-28

ADAPTATION TO VESTIBULAR DISORIENTATION. X. MODIFICATION OF VESTIBULAR NYSTAGMUS AND "VERTIGO" BY MEANS OF VISUAL STIMULATION

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October 1968

Department of Transportation
FEDERAL AVIATION ADMINISTRATION
Office of Aviation Medicine

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I. Introduction.

That visual fixation on still objects can markedly reduce an ocular nystagmus of vestibular origin was recognized by such early workers as Barany, Abels, Bartels, and Frenzel, all of whom developed or recommended special glasses to prevent fixation during clinical examinations. In experimental evaluations of the influence of vision on vestibular responses, Dodge[7] reported that (a) opportunities for still-fixation during angular acceleration resulted in a reduction only in the amplitude of nystagmus, and (b) viewing the environment during rotation produced an optokinetic nystagmus which immediately gave way to the vestibular response upon darkening the field. Mowrer[13] examined post-rotational nystagmus in a lighted room and compared the effects both of permitting vision (which generated optokinetic responses) and of excluding vision during the period of rotation. He reported much briefer and less vigorous post-rotational responses following the visual stimulation and credited these effects to the "post-stimulus persistence tendency" of the optokinetic nystagmus (which opposed the post-rotational vestibular response).

The assistance of Billy P. Updegraff, David J. Schroeder, Ruth Ann Mertens, and Alice Ramsey is gratefully acknowledged.

Ohm[15] demonstrated that still-fixation following a period of rotation inhibited the post-rotation nystagmus, while Wendt[17] reported that the response could be quickly reestablished during a subsequent period of darkness. Guedry[8] and Brown and Guedry[2] found attenuation in the duration of the oculogyral illusion as a result of introducing room illumination for a short interval following rotatory stimulation.

Guedry, Collins and Sheffey[10] confirmed the inhibition both of nystagmus and of the sensation of motion by means of a brief period of room illumination following a brisk deceleration; they also noted that the rotatory sensation showed little or no recovery during a subsequent period of darkness, whereas nystagmus was restored, albeit incompletely. More recently, it has been demonstrated that both control of balance and rapid suppression of nystagmus in figure skaters are achieved by means of visual still-fixation following on-ice spins.[4] In a comparison of figure skaters and ordinary subjects in the laboratory, active fixation on wall markers was required for 3–sec periods of room illumination which followed various deceleration stimuli; the trials were otherwise in total darkness.[5] For both groups of subjects visual fixation produced a suppression of nystagmus and of the sensation of motion; during the subsequent period of darkness (a) the subjective reaction was reinstated (although markedly reduced) in only 1 of 48 cases among the skaters and in only 17 of 48 cases among the other subjects, (b) nystagmus recommenced but clearly was not restored to the level of an uninterrupted response, (c) the duration of the primary nystagmus was significantly shorter than that of an uninterrupted response, and (d) an enhanced secondary nystagmus appeared. Although the report does not clearly define his test procedure, Markaryan[12] also noted strong secondary nystagmic reactions after angular stimulation during eye closure following a period of visual fixation.

The present study was undertaken to examine further the influence of visual information on vestibular responses. Particular attention was directed toward the occurrence and characteristics of secondary vestibular reactions resulting from variations in the type and timing of the visual input.

II. Method.

Subjects. Four groups were tested in the Stille-Werner Rotation Device. Groups A, B, and C each comprised six subjects; thirteen of these were males, five were females. Group D comprised twelve male subjects. All subjects were paid volunteers between 21-27 years of age.

Recording. Surface electrodes were taped by the outer canthi of each subject's eyes to record horizontal components of eye movements. A ground electrode was clipped to the ear lobe. Recording was accomplished by means of an Offner Type T polygraph with RC time constants of 3 sec used in amplification. Subjects

The experimental trials differed among the

to the recorder, by means of which they could signal onset and direction of turning, each 90° turn which they experienced, and the termination of their sensations.

Procedure. Subjects were seated in the rotation device with their eyes open and their heads upright but anteverted so that the lateral semicircular canals were approximately in the plane of rotation. They were instructed in detail regarding the signalling of turning experiences and were given two familiarization trials in total darkness. These trials, alternately CW and CCW, consisted of accelerations and decelerations of $5°/sec^2$ for 12 sec separated by a 2-min period of constant velocity.

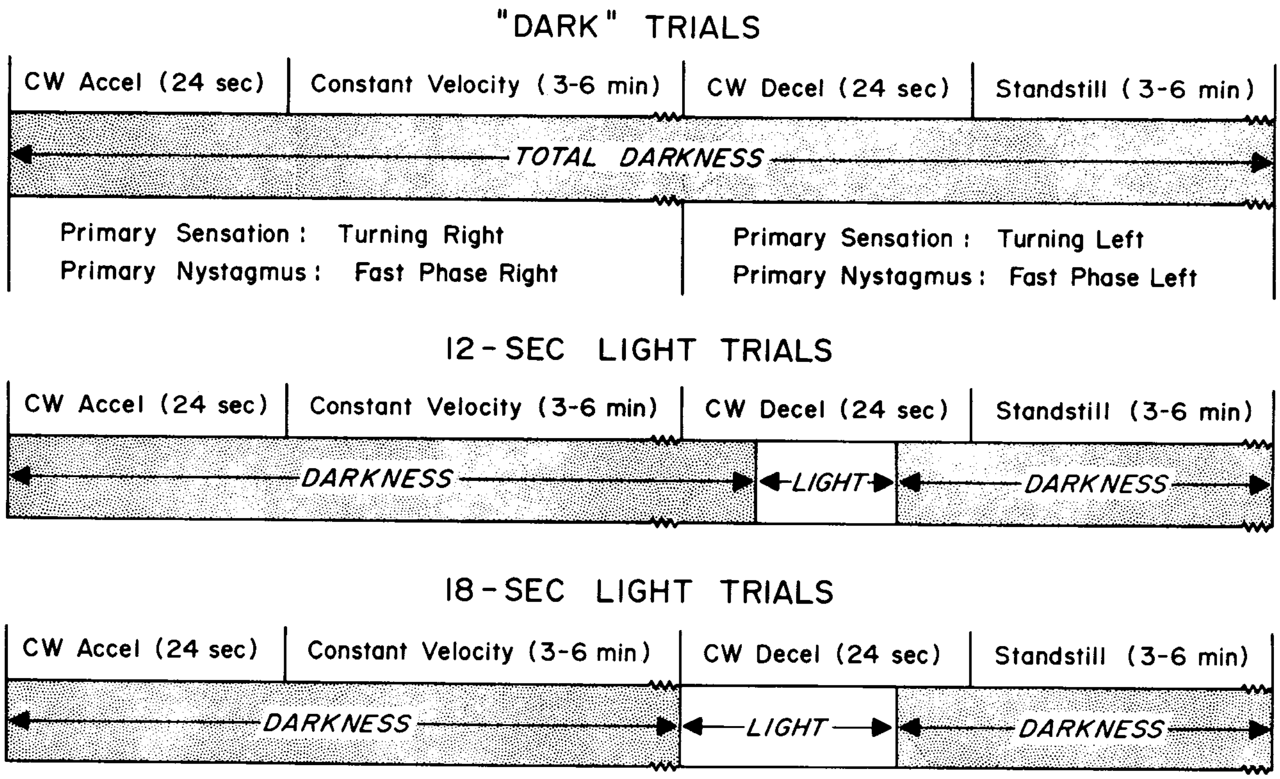

FIGURE 1. Test conditions used for Groups A, B, and C.

groups. Subjects in Groups A and B each received 6 trials; 3 trials were conducted in total darkness and 3 trials involved the introduction of a period of room illumination during the deceleration (see Figure 1). For these groups a "dark" and a "light" trial were run with stimulus rates of $1°/sec^2$, $3°/sec^2$, and $5°/sec^2$. In all cases rotation was CW and the stimulus duration was 24 sec. Accelerations and decelerations were provided with two microswitches, connected

were separated by periods of 3-6 min of constant velocity, depending primarily on the presence of secondary nystagmus. Time at a standstill from the end of deceleration to the start of the next acceleration ranged from 6–9 min, again depending upon the presence of secondary reactions. At least 3 min were spent in room illumination prior to the start of each trial. A modified counterbalancing of stimulus presentations was used, as indicated in Table 1, with a "dark" trial always preceding the "light" trial for a given magnitude of angular stimulus.

"Dark" trials were the same for Groups A and B; the "light" trials differed with respect to visual conditions during deceleration (see Figure 1). The "light" trial decelerations for Group A began with a 6-sec period of total darkness followed by 12-sec of full-room illumination (during which the subject saw his direction and slowing speed of angular motion); the remaining 6 sec of deceleration and a period of 3-6 min at a standstill were in total darkness. For Group B, the first 18 sec of deceleration occurred in full-room illumination, followed by 6 sec of decelera-

TABLE 1. Order of stimulus presentation for Groups A and B. Acceleration and deceleration stimuli were always 24 sec in duration. "Dark" trials were in total darkness; "light" trials were in darkness with the exception of the middle 12 sec of the deceleration period for Group A and the first 18 sec of deceleration for Group B, during which time the room was illuminated. For a given stimulus rate, a dark trial always preceded a light trial.

Subjects		Trials					
Group A (12-sec Light Trials)	Group B (18-sec Light Trials)	1 Dark	2 Light	3 Dark	4 Light	5 Dark	6 Light
BM	BR	1°/sec²		3°/sec²		5°/sec²	
AW	MH	3°/sec²		5°/sec²		1°/sec²	
RM	MK	5°/sec²		1°/sec²		3°/sec²	
RR	LT	1°/sec²		5°/sec²		3°/sec²	
LM	LM	3°/sec²		1°/sec²		5°/sec²	
TB	JH	5°/sec²		3°/sec²		1°/sec²	

TABLE 2. Order of stimulus presentation for Group C. Acceleration and deceleration stimuli was always 24 sec in duration. "Dark" trials were in total darkness; other trials were in darkness with the exception of the middle 12 sec of the deceleration period or the first 18 sec of the same period, during which time the room was illuminated. Subjects received three trials each at 3°/sec² and 4°/sec² with the deceleration conditions presented in the order listed.

Subject	Trials	Rate (°/sec²)	Deceleration Conditions
JB	1-3	3	18-sec light; 12-sec light; dark
	4-6	4	12-sec light; 18-sec light; dark
DG	1-3	3	dark; 18-sec light; 12-sec light
	4-6	4	18-sec light; 12-sec light; dark
MD	1-3	4	dark; 18-sec light; 12-sec light
	4-6	3	12-sec light; 18-sec light; dark
MC	1-3	4	18-sec light; dark; 12-sec light
	4-6	3	12-sec light; dark; 18-sec light
JS	1-3	3	dark; 12-sec light; 18-sec light
	4-6	4	12-sec light; dark; 18-sec light
PC	1-3	4	dark; 12-sec light; 18-sec light
	4-6	3	18-sec light; dark; 12-sec light

TABLE 3. Order of stimulus presentation for Group D. Stimuli were 3°/sec² for 20 sec and 10°/sec² for 12 sec. Dark trials were in total darkness. Other trials were in darkness with the exception of (a) the first 14 sec of the 3°/sec² deceleration, (b) the first 6 sec of the 10°/sec² deceleration, (c) 3–sec periods beginning one sec after the termination of deceleration while the subject was at a standstill (stst); during these intervals the room was illuminated. Subjects received three trials each at 3°/sec² and at 10°/sec² with the deceleration conditions presented in the order listed. For half of the subjects, trials 1-3 were at 3°/sec² and trials 4-6 were at 10°/sec²; the order was reversed for the remaining six subjects.

				Stimulus	
Subject	*Trials*	*Subject*	*Trials*	*Rate (°/sec²)*	*Deceleration Conditions*
BD	1-3	JP	4-6	3	dark; 14-sec light; 3-sec light (stst)
	4-6		1-3	10	dark; 6-sec light; 3-sec light (stst)
GL	1-3	ML	4-6	3	14-sec light; 3-sec light (stst); dark
	4-6		1-3	10	6-sec light; 3-sec light (stst); dark
PH	1-3	DV	4-6	3	3-sec light (stst); dark; 14-sec light
	4-6		1-3	10	3-sec light (stst); dark; 6-sec light
RW	1-3	BI	4-6	3	dark; 3-sec light (stst); 14-sec light
	4-6		1-3	10	dark; 3-sec light (stst); 6-sec light
CP	1-3	RK	4-6	3	14-sec light; dark; 3-sec light (stst)
	4-6		1-3	10	6-sec light; dark; 3-sec light (stst)
RM	1-3	CH	4-6	3	3-sec light (stst); 14-sec light; dark
	4-6		1-3	10	3-sec light (stst); 6-sec light; dark

tion and 3–6 min at a standstill in total darkness. Groups A and B thus differed in two respects: (1) Group B was exposed to a longer period of room illumination during decelerations (18 sec vs. 12 sec); (2) Group A could experience motion to the left during the first 6 sec of deceleration (in darkness) and then have this perception visually corrected during illumination of the room, whereas Group B was exposed to illumination at the moment the deceleration began, and thus could not have an initial sensation of turning to the left.

To clarify some results obtained from Groups A and B, Group C was given trials (a) in total darkness, (b) with the 12–sec light period, and (c) with the 18–sec light period, at stimulus rates of 3°/sec² and 4°/sec² for 24 sec durations. A counterbalanced order of presentation was used as indicated in Table 2.

Group D provided additional information regarding the influence of visual stimulation on vestibular responses. For complete assurance that the subjects were not influenced by breeze cues, a small cabin with a wide window was

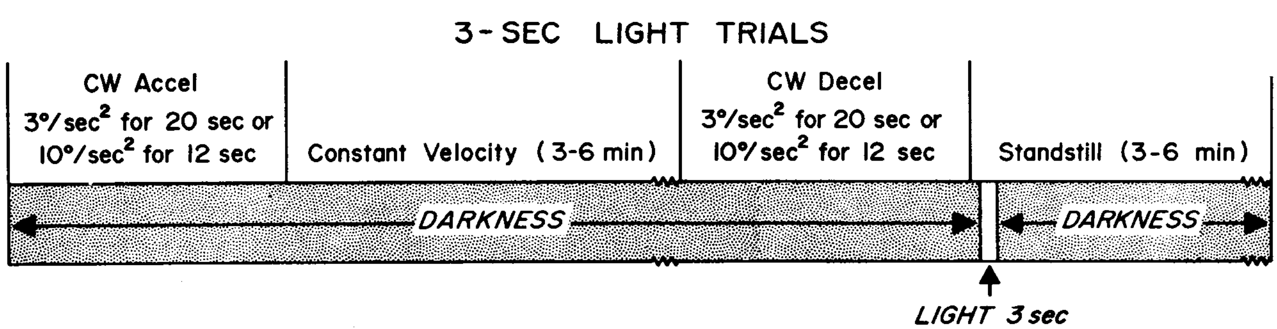

FIGURE 2. The still-fixation light condition used for Group D.

secured around the chair so that a seated subject was totally enclosed but could see the walls of the room when lights were turned on. Each of 12 subjects was exposed to 3 visual conditions at 2 stimulus rates ($3°/sec^2$ for 20 sec and $10°/sec^2$ for 12 sec) as indicated in Table 3. For both rates, subjects were rotated (a) in total darkness; (b) with room lights on during the first 14 sec ($3°/sec^2$) or first 6 sec ($10°/sec^2$) of the decelerations (i.e., similar to the 18-sec light trials depicted in Figure 1, the last 6 sec of the deceleration and the subsequent periods of standstill were in total darkness); and (c) in total darkness with the exception of a 3-sec period of room illumination beginning one sec after the end of deceleration (i.e., during the period of standstill, see Figure 2).

Subjects were instructed to signal the onset of their turning sensation by depressing the microswitch in their right hand if they perceived turning to the right, or by depressing the microswitch in their left hand if the perceived direction of turn was to the left. They then signalled each experience of turn through 90° angles and the termination of these sensations by depressing the appropriate switch. For experimental trials in which the room was illuminated during deceleration, the subjects were instructed simply to watch the room walls and when the lights were again turned off, to resume signalling any further experiences of angular motion while calling out the direction of their turning sensation. Many subjects, however, made signals during the period of light.

For trials in which the room lights were turned on for 3 sec during the period of standstill following deceleration (Group D only), subjects were told actively to fixate on wall markers during the interval of light and to resume signalling their sensations when the lights went out.

Since all experimental trials were rotations in a CW direction, subjects experienced turning to th left at an increasing rate during decelerations in total darkness; during periods of room illumination during deceleration, they could see that the direction of rotation was to the right and that the velocity of turning was decreasing. The deceleration stimulus in darkness also produced nystagmus with fast-phase to the left; with illumination of the room during deceleration, an optokinetic nystagmus was produced with fast-phase to the right.

Scoring. Only deceleration data were scored. Tracings were marked off in 3-sec intervals (backwards through the stimulus period and forward through the post-rotatory period) from the point at which the deceleration ended and the chair reached a complete standstill. Slow-phase eye deviation was measured by summing the slow-phase displacements of each nystagmic beat, from peak to base-line, in each 3-sec interval. These values were converted to degrees of eye movement with a calibration factor obtained prior to each trial (subjects moved their eyes through a known arc across a specially constructed device). Subjective responses were also scored in 3-sec intervals. Since each signal represented 90° of experienced angular movment, degrees of apparent displacement were readily calculated.

III. Results and Discussion.

Groups A, B, AND C

Nystagmus. Mean slow-phase measures for Groups A and B were plotted in Figures 3, 4, and 5 for stimulus magnitudes of $1°/sec^2$, $3°/sec^2$, and $5°/sec^2$, respectively. For each group a "dark" and a "light" trial were plotted on the same graph for comparison purposes.

Data for Groups A and B were similar. During "dark" trials a rise in nystagmic output generally occurred throughout the deceleration stimulus followed by a response decay during the period of standstill. Primary nystagmus eventually gave way to generally weak secondary nystagmus in 24 of the 36 "dark" trials. During "light" trials, primary vestibular nystagmus quickly replaced the optokinetic responses generated by watching the walls of the room during part of the deceleration, increased during the remaining 6 sec of stimulus in total darkness, and then decayed in the standstill period. The primary response following the period of room illumination was clearly of lower magnitude than that which occurred during comparable time periods in the "dark" trials, i.e, although primary nystagmus recommenced in the dark following the interval of light, it did not reach the output-level of the "dark-trial" responses. Further, the duration of the primary response was significantly shorter and the onset of the secondary re-

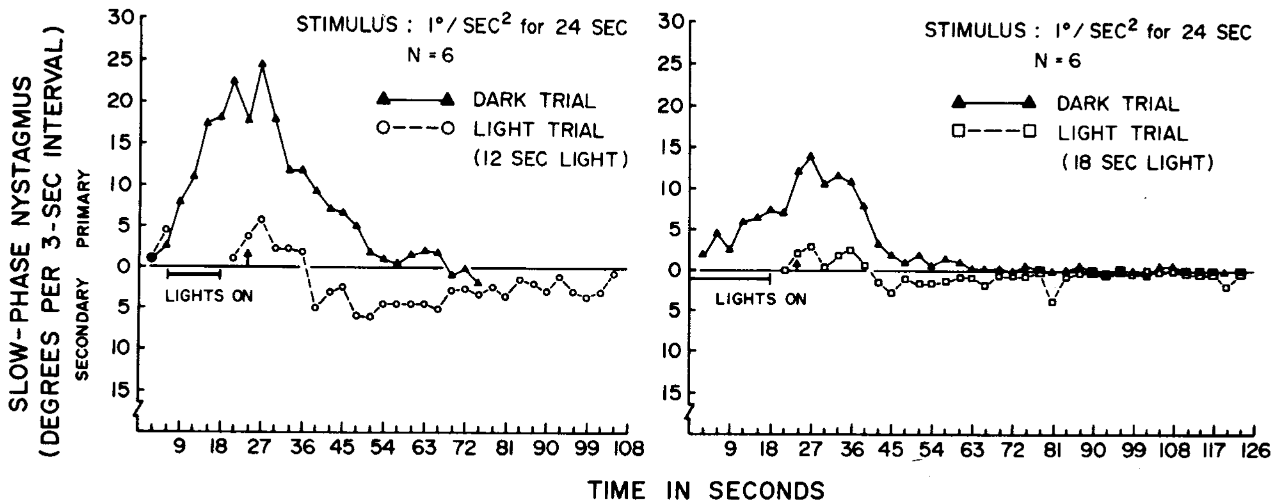

FIGURE 3. Average slow-phase nystagmus for "dark" and for "light" trial decelerations of 1°/sec² for Group A (12-sec light) and Group B (18-sec light). Primary nystagmus is plotted above the zero line, secondary nystagmus below that line. Arrows indicate termination of the stimuli. Horizontal bars beneath the zero line demarcate the periods of full-room illumination during deceleration. Nystagmus (optokinetic) was not scored during the interval of light.

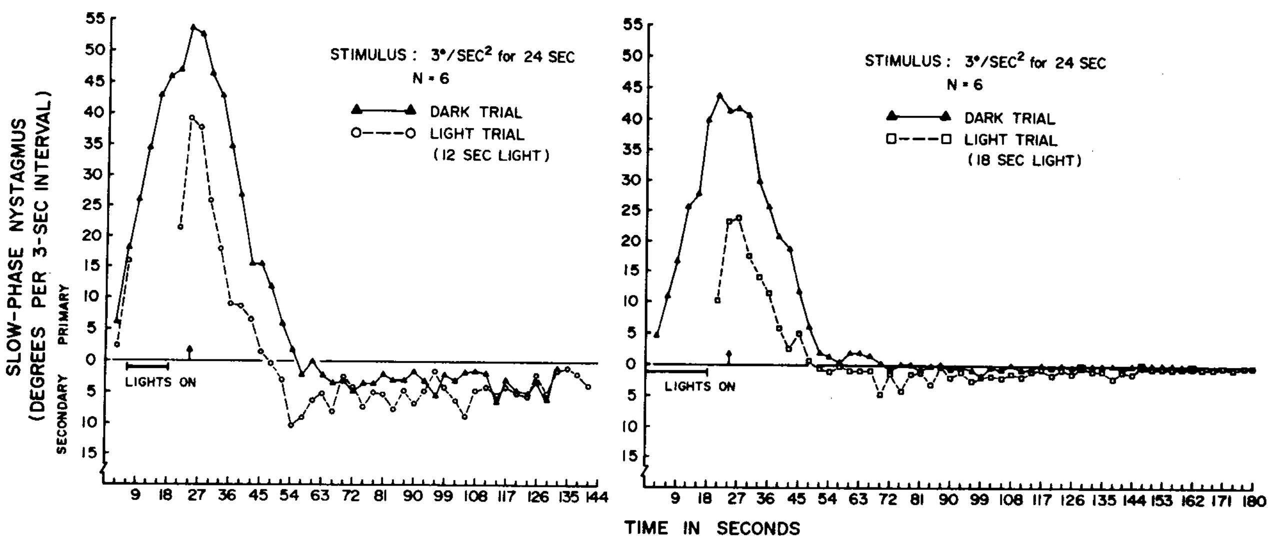

FIGURE 4. Average slow-phase nystagmus for "dark" and for "light" trial decelerations of 3°/sec² for Group A (12-sec light) and Group B (18-sec light). Markings are the same as in Figure 1.

sponse significantly earlier (.05–.01 levels by t tests) for "light" trials as compared with "dark" trials for the 2 groups, with the exception of the 5°/sec² stimulus for Group A. Secondary nystagmus occurred more frequently (in 33 of the 36 "light" trials) and also showed greater overall output in 27 of the 36 comparisons with "dark" trials (particularly in comparing the first 30 sec of the response).

Group C provided a direct comparison of the effects on nystagmus of the 12-sec and 18-sec light periods (see Figure 6). As in Groups A and B, comparisons of "dark" with "light" trials showed that, for "light" trials: (a) primary nystagmus was clearly of lower magnitude; (b) the primary response was significantly shorter and the onset of the secondary response (which occurred in 23 of 24 "light" trials and in 11 of 12 "dark" trials) was significantly earlier (.05 levels by t tests); and (c) the overall amount of secondary nystagmus was greater in 21 of the 24 comparisons. However, there were

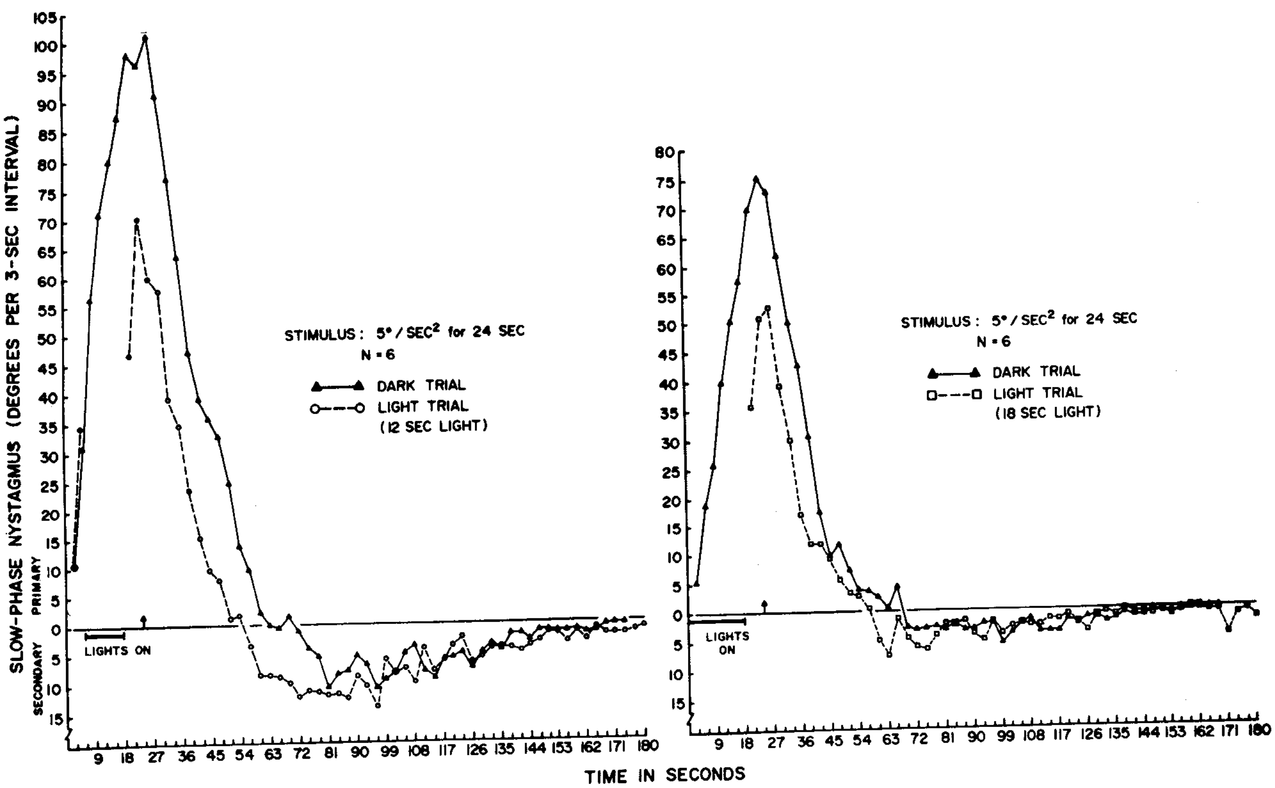

FIGURE 5. Average slow-phase nystagmus for "dark" and for "light" trial decelerations of 5°/sec² for Group A sec light) and Group B (18-sec light. Markings are the same as in Figure 1.

no statistically significant differences between the 2 "light" trials for these measures.

Subjective Reactions. The signals indicating experience of turning through 90° angles were scored, like nystagmus, in 3-sec intervals.[3] The data for Groups A and B were plotted in Figures 7, 8, and 9 for stimulus magnitudes of 1°/sec², 3°/sec², and 5°/sec², respectively. Data for Group C appear in Figure 10.

"Dark" trials. For Groups A and C, the subjective rate of turning (to the left) increased throughout the deceleration stimuli and then decayed. Secondary turning sensations were experienced only occasionally in all 3 groups with no more than 2 subjects reporting these reactions at any given stimulus magnitude (see Table 4). For Group B, an increasing rate of turning in total darkness was experienced for the first 18–21 sec of the 24-sec deceleration for all 3 stimulus magnitudes; however, a response decline consistently began during the last 3–6 sec of the decelerations and continued during the period of standstill. A decay in the subjective reaction (adaptation) during a prolonged stimulus is not an unusual finding and has been examined in detail elsewhere.[11]

"Light" trials. The intervals of room illumination during "light" trial decelerations markedly influenced the reported subjective reactions. On an overall basis, 11 of 18, 14 of 18, and 23 of 24 "light" trials for Groups A, B, and C, respectively, produced responses in the direction of a secondary sensation (see Table 4). Most striking, however, was the fact that in 7 Group A trials, in 12 Group B trials, and in 20 Group C trials, the "secondary" sensation of turning to the *right* began during the last 6 sec of deceleration in darkness (following the period of light). That is, although the semicircular canals were signalling a sensation of turning to the left during deceleration (and a left-beating nystagmus had recommenced), the visual information obtained during the period of room illumination, which indicated actual turning to the right at a decreasing rate, apparently corrected the directional component of the sensation during the subsequent dark period. For Groups A and B the 3°/sec² stimulus appeared somewhat more effec-

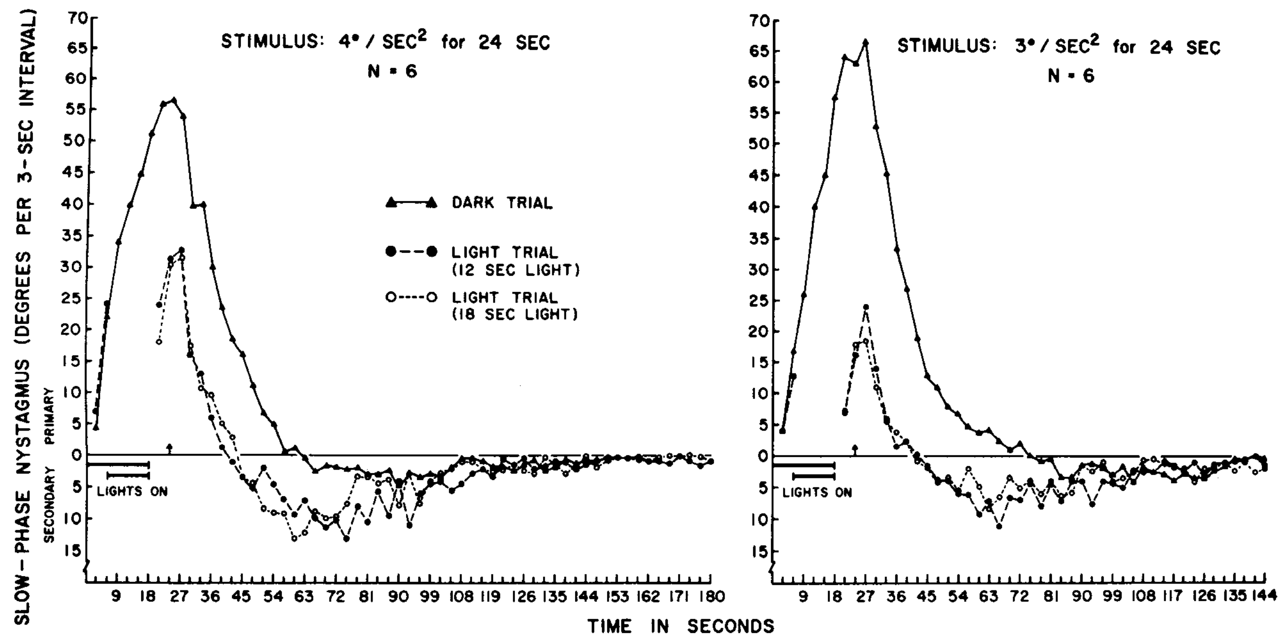

FIGURE 6. Average slow-phase nystagmus for "dark" and for "light" trial decelerations of 3°/sec² and 4°/sec² for Group C. Markings are the same as in Figure 1.

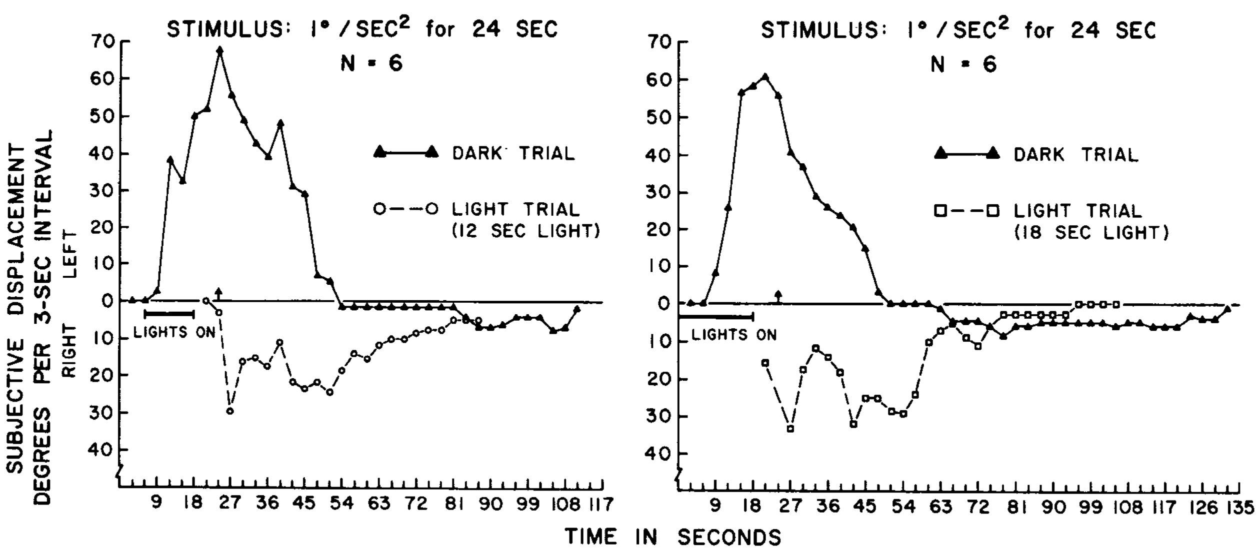

FIGURE 7. Average subjective displacement in degrees of experienced turning for "dark" and for "light" trial decelerations of 1°/sec² for Group A (12-sec light) and Group B (18-sec light). Markings are similar to those in Figure 1. The primary sensation to the CW decelerations in darkness would be rotation to the left; visual information during the periods of light frequently produced reversals in the perceived direction of turning during the subsequent periods of darkness.

tive in this regard than either the 1°/sec² or the 5°/sec² decelerations. At the 5°/sec² stimulus level, there was more of a tendency for the primary raction (apparent rotation to the left) to occur during the last 6 sec of the stimulus or following stimulus termination, i.e., at the highest stimulus magnitude the vestibular signals appeared more effective in reinstating the primary subjective reaction following the period of room illumination. For Group C, the 3°/sec² and 4°/sec² stimuli were equally effective in eliciting "secondary" sensations during the 6 sec of deceleration following the light interval.

Group D

Nystagmus. Mean slow-phase nystagmus was plotted in Figure 11. During "dark" trials, nystagmic output increased throughout the deceleration stimuli, decayed during the periods of standstill, and gave way to secondary responses in 21 of the 24 trials. The introduction of room illumination, whether it was during or immediately following deceleration, sharply reduced the magnitude of the primary response. In comparison with "dark" trials, the primary response to "light" trials was significantly shorter and the onset of secondary nystagmus occurred significantly sooner (.001 levels by t tests). Secondary nystagmus appeared in all "light" trials and was of greater overall output (especially during the initial 45 sec) than that of the "dark" trials in 32 of the 48 comparisons.

For the 10°/sec² stimulus, there were no significant differences between the two types of "light" trials with regard to duration of primary, onset of secondary, and magnitude of secondary nystagmus. For the 3°/sec² stimulus, primary nystagmus ended earlier and secondary nystagmus began sooner (.001 levels) in the 14–sec "light" trials as compared with the 3–sec "light" trials; the magnitude of the secondary reaction was also greater, but not significantly so.

Subjective Reactions. Figure 12 depicts the time-course of the subjective reactions for Group D. "Dark" trials showed an increasing rate of experienced turn throughout the stimulus followed by a decay in the primary reaction during

TABLE 4. Subjective data from Groups A, B, and C. The number of subjects experiencing primary and secondary sensations is indicated for "dark" and for "light" trials. The heading "During Decel" refers to the final 6 seconds of deceleration (always in darkness). During the standstill period following deceleration, primary responses sometimes were succeeded by secondary reactions.

			During Decel		*Following Decel*	
Trials	*°/sec²*	*N*	*Primary*	*Secondary*	*Primary*	*Secondary*
Group A						
Dark	1	6	6	0	6	2
	3	6	6	0	6	1
	5	5*	5	0	5	0
12-sec	1	6	0	2	0	3
Light	3	6	0	4	1	4
	5	6	2	1	3	4
Group B						
Dark	1	6	6	0	6	1
	3	5**	5	0	5	0
	5	6	6	0	6	2
18-sec	1	6	0	4	0	4
Light	3	6	0	5	0	5
	5	6	2	3	3	5
Group C						
Dark	3	6	6	0	6	1
	4	5**	5	0	4	1
12-sec	3	6	0	5	0	6
Light	4	6	0	5	0	6
18-sec	3	6	0	5	0	5
Light	4	6	0	5	0	6

*One subject was excluded due to mechanical failure of a microswitch.
**One subject was excluded for failure to provide complete signals.

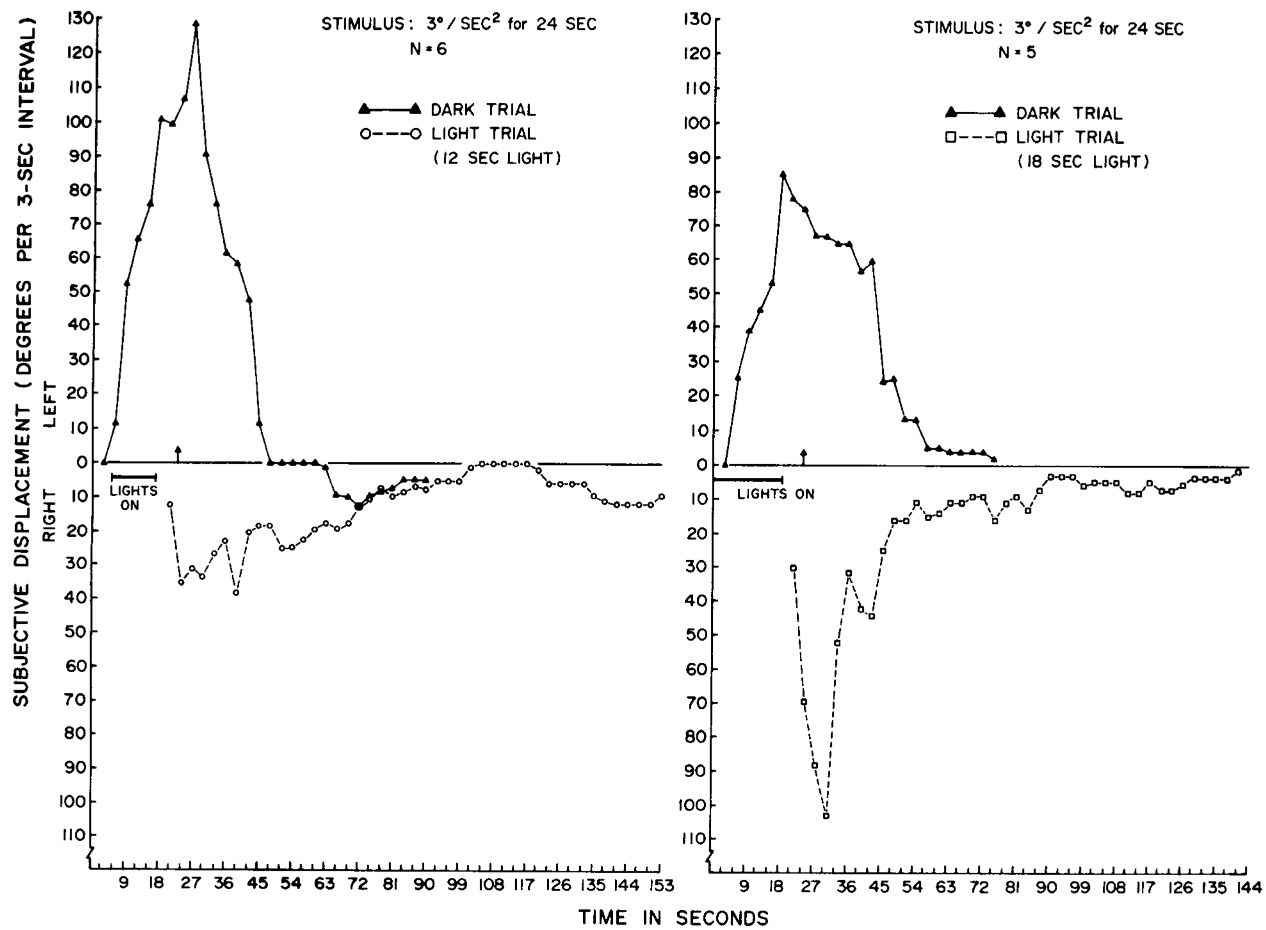

FIGURE 8. Average subjective displacement in degrees of experienced turning for "dark" and for "light" trial decelerations of 3°/sec² for Group A (12-sec light) and Group B (18-sec light). Markings are similar to those in Figure 1. Results are comparable to findings in Figure 7. One subject from Group B was not included in data averages due to his failure to provide complete signals during the "dark" trial.

the period of standstill. Secondary reactions were reported by 2 subjects for the 3°/sec² rate and by 5 subjects for the 10°/sec² rate. Introduction of the room lights during the first part of the deceleration periods resulted in 9 reports of secondary reactions following the 3°/sec² stimulus and in 10 such reports following the 10°/sec² stimulus. Five of the former and 6 of the latter began *during* the last 6 sec of the deceleration (see Table 5). The 3 sec of room illumination with the chair at a standstill resulted in no subsequent sensation for 5 subjects following the 3°/sec² deceleration and in secondary sensations for the remaining 7 subjects. At 10°/sec², weak primary sensations which gave way to strong secondary reactions followed the period of still fixation in 5 subjects; 6 others had only secondary sensations while the remaining subject reported no experience of motion subsequent to the 3–sec light interval. These data support the results from Groups A and B in that at higher stimulus magnitudes the primary sensation is often reinstated (albeit weakly) following periods of visual information, whereas at lower rates the primary sensation is almost always suppressed (Tables 4 and 5).

IV. General Discussion.

Nystagmus. The present data support previous reports which demonstrated a reduction of postrotatory primary nystagmus as a result either of visual still-fixation or of opposing optokinetic stimulation during angular accelerations. As Dodge[7] and Wendt[17] noted, the primary reaction is quickly reestablished during a period of darkness subsequent to a period of visual stimulation, but the present data indicate that it clearly does not return to the level of an uninterrupted response (see also[10]). The "post-stimulus persistence tendency" of optokinetic reactions by which Mowrer[13] explained his findings is not sufficient to account for these results since still-fixation on stationary objects also produced attenuation of nystagmus.

Of particular interest is the fact that vigorous secondary ("post-post") nystagmic reactions so frequently followed the reduced primary response during "light" trials. This enhanced (as compared with "dark" trials) secondary nystagmus apparently can be triggered not only by still-fixation as reported earlier[5] but also by opposing optokinetic impulses during vestibular stimulation.

Secondary nystagmus is considered to be of central origin[1] and may occur as a result of "prolonged" neutral activity in the primary direction.[5] Whether the secondary response is the result of an induced central imbalance or is initiated to oppose the primary nystagmus, it appears that at least some types of visual informa-

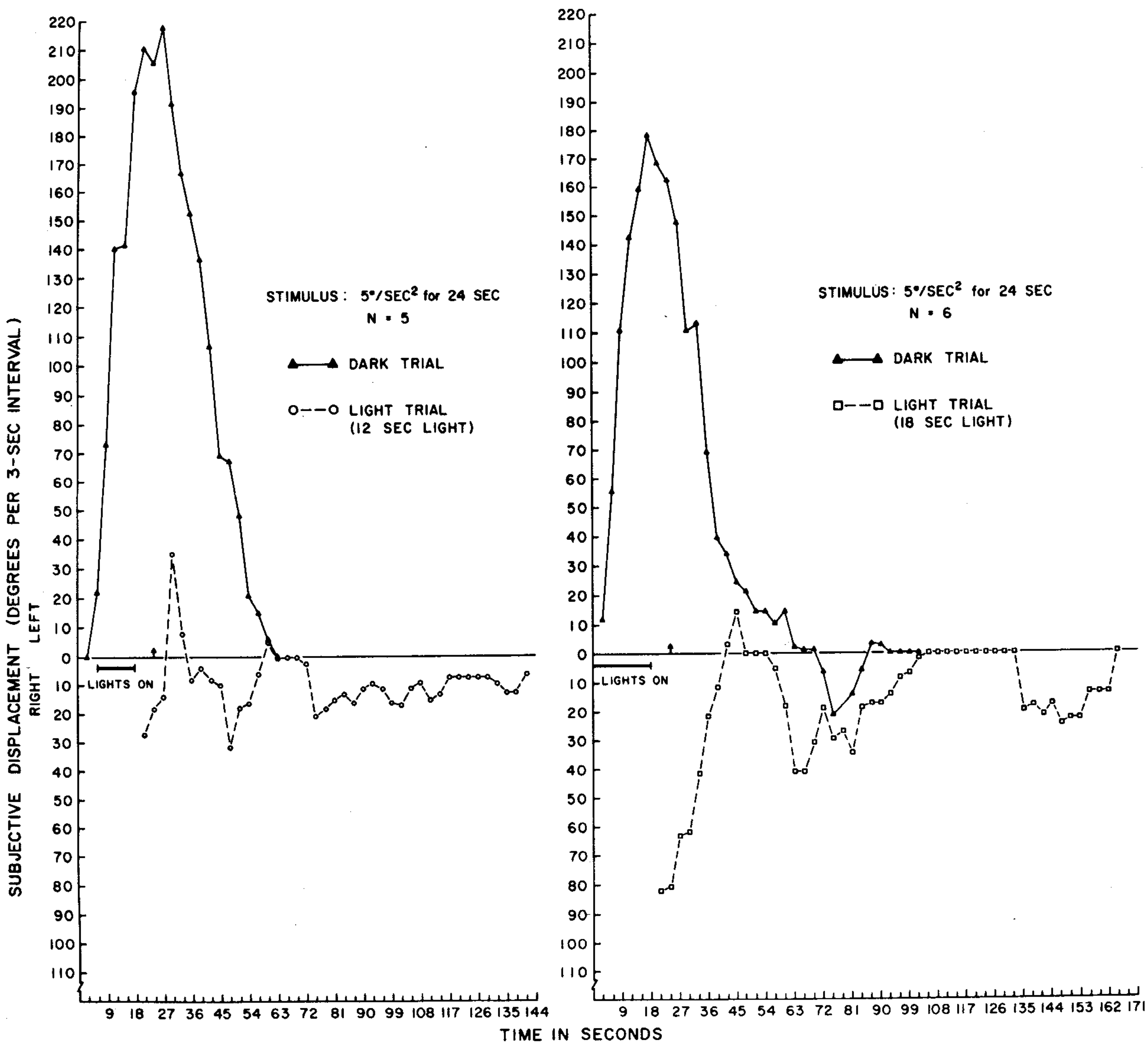

FIGURE 9. Average subjective displacement in degrees of experienced turning for "dark" and for "light" trial decelerations of 5°/sec² for Group A (12-sec light) and Group B (18-sec light). Markings are similar to those in Figure 1. Results are comparable to findings in Figures 7 and 8. One subject from Group A was not included in data averages due to a malfunction of his signalling device during a "dark" trial.

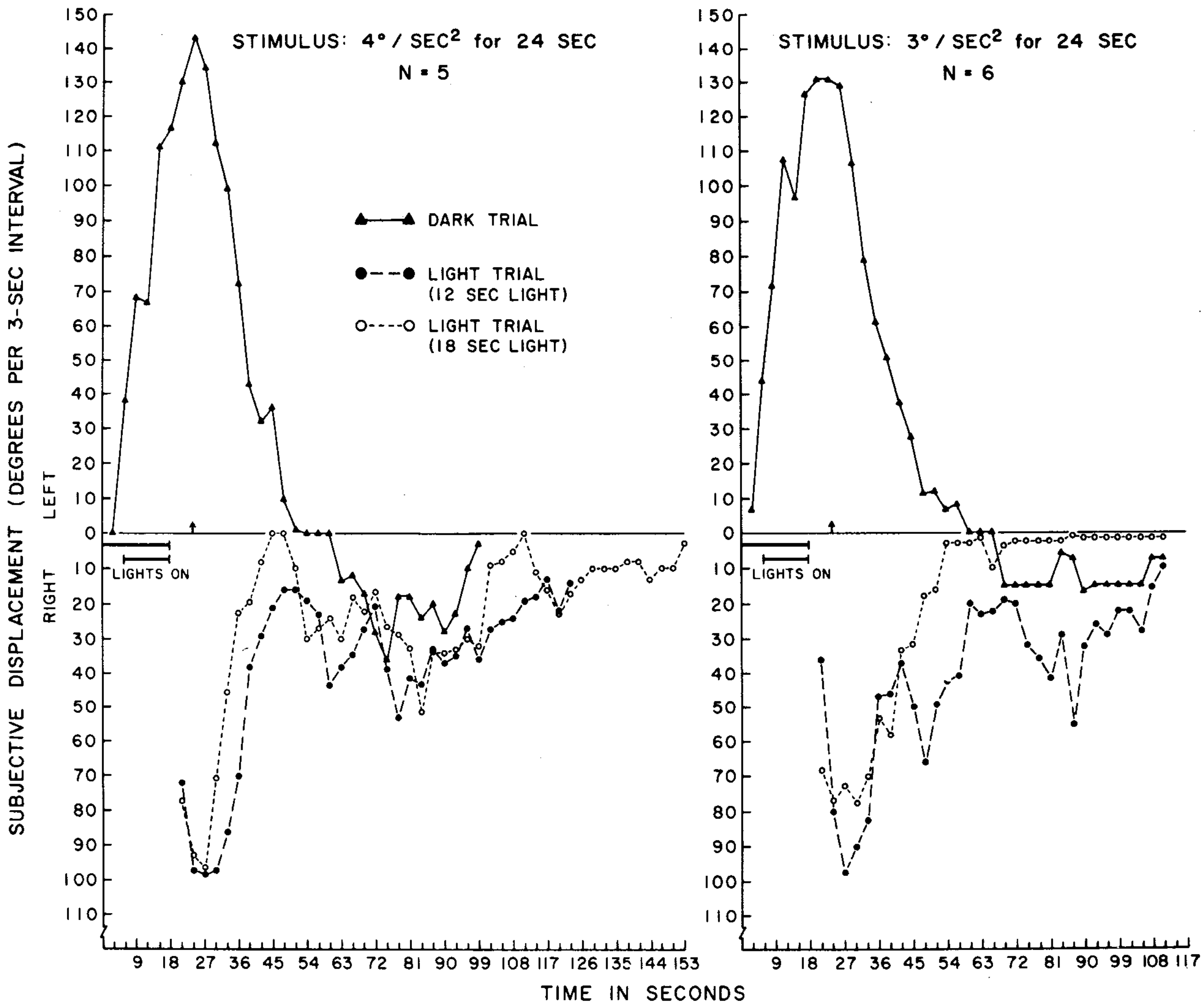

FIGURE 10. Average ssubjective displacement in degrees of experienced turning for "dark" and for "light" trial decelerations of 3°/sec² and 4°/sec² for Group C. Markings are similar to those in Figure 1. One subject was not included in data averages for the 4°/sec² stimulus due to his failure to provide complete signals during the "dark" trial. Compare with Figures 7, 8, and 9.

tion can be centrally integrated and enhance this ongoing, opposed reaction.

The above view may also account for those cases (25% of the comparisons) in which less secondary nystagmus was demonstrated (although the responses were still strong) following room illumination than during trials in total darkness. Subjects in this category appeared to share two characteristics: on the average, they had (1) more primary nystagmus (slow-phase displacement) and (2) more secondary output during their "dark" trials as compared with subjects whose secondary mystagmus was increased following periods of room illumination. For both of these subject-groupings, the introduction of visual stimulation reduced the primary nystagmic output by approximately the same proportions but, of course, the amount of the reduction was greater for one group than for the other. It is possible that a combination of high primary and secondary output in total darkness reflects a delay in the release of the secondary reaction. Thus, the primary responses may be relatively unopposed (and therefore high in magnitude) while the secondary response, being released relatively late (perhaps very near the end of the primary nystagmus), may appear particularly vigorous. In these cases, visual information during primary reactions actually may enhance the vigor of the opposed process but may also serve to trigger its release earlier thereby exhausting some of this previously contained energy, reducing the primary output, and resulting in relatively less observable secondary nystagmus. An early release of the opposed process may characterize those cases (75% of the comparisons) in which secondary nystagmus was enhanced during "light" trials and generally weak or absent during trials in total darkness. Here the primary response in "dark" trials may be relatively less vigorous due to the early release of the opposed process. The latter is then "used up" during most of the primary reaction and yields weak observable secondary reactions. In these cases, visual information may enhance the opposed reaction, reduce the primary nystagmus, and produce a stronger secondary nystagmus. It is also possible that differences among subjects in the release time of the opposed reactions may be related to susceptibility to habituation or to motion sicknss. In this regard, Preber[16] has reported that pilot trainees who became severly airsick during flight training showed, prior to training, longer durations of nystagmus and turning sensations and greater maximum eye speed of nystagmus resulting from laboratory rotations than did pilot trainees who did not get airsick. A follow-up of 6 subjects who overcame airsickness and completed the flight course showed that post-training measures

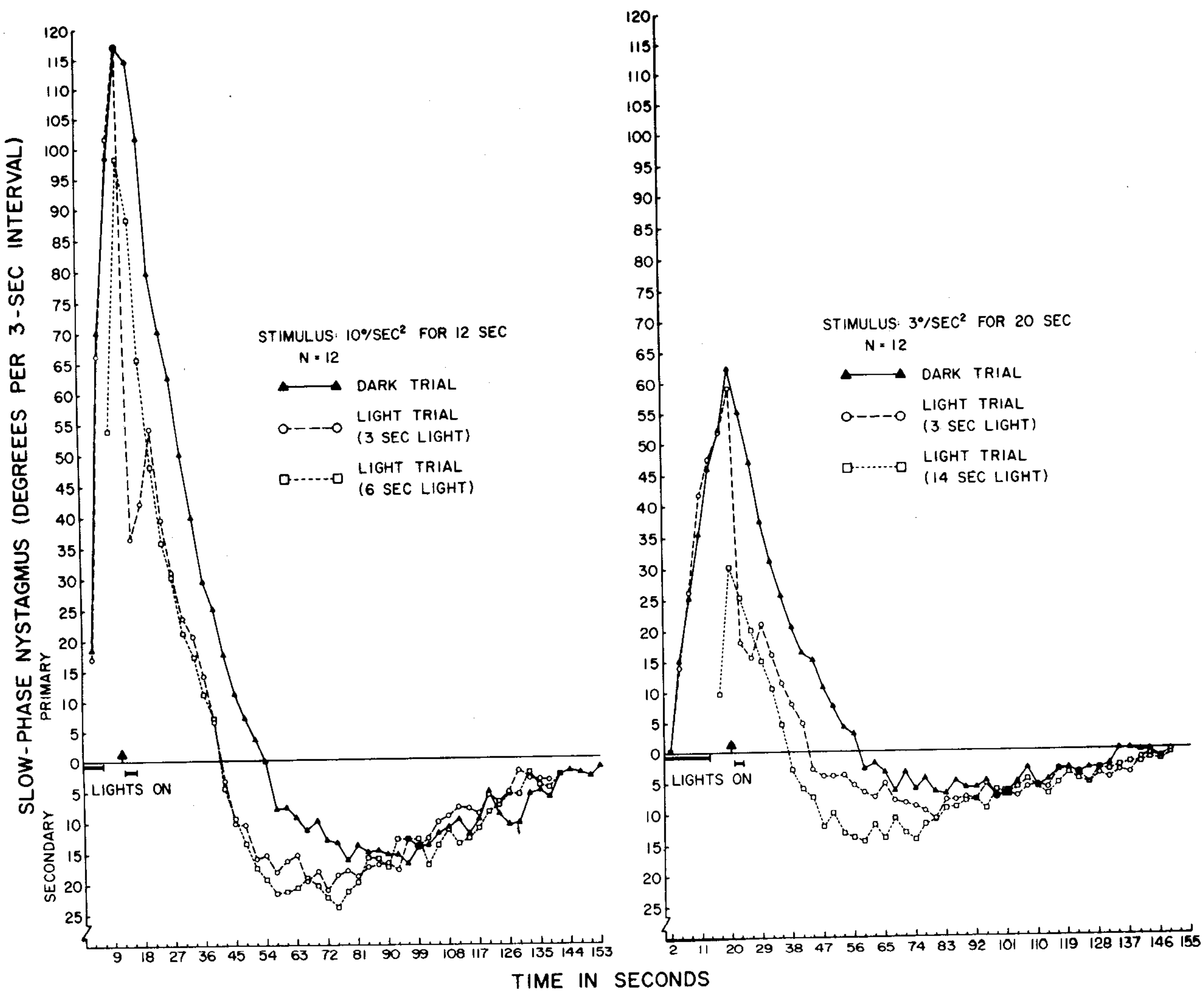

FIGURE 11. Average slow-phase nystagmus for "dark" and for "light" trial decelerations of 3°/sec² and 10°/sec² for Group D. Markings are the same as in Figure 1.

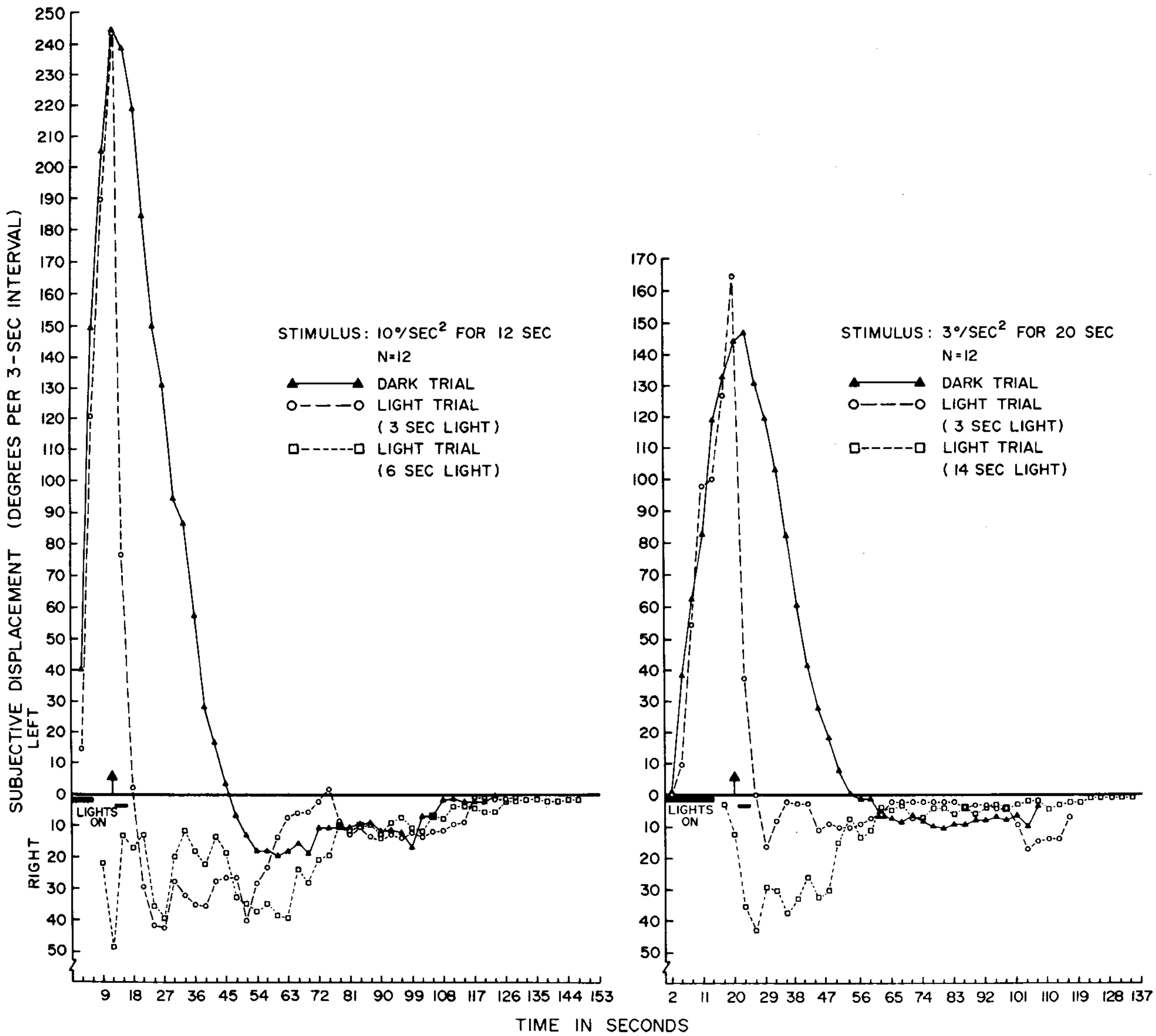

FIGURE 12. Average subjective displacement in degrees of experienced turning for "dark" and for "light" trial decelerations of 3°/sec² and 10°/sec² for Group D. Markings are similar to those in Figure 1.

TABLE 5. Subjective data from Group D. The number of subjects experiencing primary and secondary sensations is indicated for "dark" and for "light" trials. The heading "During Decel" refers to the final 6 seconds of deceleration (always in darkness). Room illumination wasprovided during the deceleration periods for the 14-sec light (stimulus duration: 20 seconds) and 6–sec light (stimulus duration: 12 seconds) trials, and one second after the end of deceleration (while at a standstill) for the 3-sec light trials.

			Group D			
			During Decel		*Following Decel*	
Trials	*°/sec²*	*N*	*Primary*	*Secondary*	*Primary*	*Secondary*
Dark	3	12	12	0	12	2
	10	12	12	0	12	5
3-sec light	3	12	12	0	0	7
(Standstill)	10	12	12	0	5	11
14-sec light	3	12	1	5	2	9
6-sec light	10	12	1	6	3	10

of both sensations and nystagmus had undergone reductions from pre-training levels.

Subjective Reactions. In previous studies, when subjects were permitted briefly to see that they were stationary shortly after the termination of angular deceleration, further sensations of turning during subsequent periods of darkness were either markedly reduced or were terminated.[5,10] Secondary sensations, however, were not reported to occur probably due to a combination of the type of subjects used, the timing of the period of permitted vision, and a failure to seek such information from the subjects. Whether visual information regarding stationary objects is provided during a deceleration stimulus or while at a period of standstill (in either event, when it is in conflict with the vestibular signals), it seems clear that secondary sensations occur much more frequently and are usually more vigorous than when vestibular stimulation occurs entirely in darkness.

That strong secondary sensations occur following such visual stimulation is perhaps not so surprising in view of the similar effects that the same type of input frequently produces on the nystagmic reaction. However, the occurrence of reversals in sensation *during* the last few seconds of deceleration in darkness following a period of room illumination is particularly striking. Many of the "secondary" sensations which began *during* the deceleration (23 of 39 for Groups A, B, and C; 2 of 11 for Group D) were relatively short in duration but were followed by another (much more intense) rise and decline of a turning sensation in the same direction (again to the right), i.e., a bimodal secondary effect was evidenced (and is apparent in many of the graphs). In these cases, the initial response appeared to have a fairly sudden onset 2 or 3 sec after the lights were turned off; velocity then increased quickly and quickly decayed. The following response (in the same direction) frequently began just a few sec later, showed a rise and decline of velocity, and was of long duration.

These brief-duration reversals of sensation during the deceleration could be the result of "suggestion" resulting from a weak, perhaps indefinite sensation of motion following the visual information, but they do not appear so. Subjects reported with conviction (calling out the direction as they signalled) and, in Groups A and B, most frequently had these experiences at the lower rates of stimulation. The latter fact also argues against the influence of breeze cues which possibly could have affected subjects in Groups A, B, and C (but not in Group D) in spite of careful instructions; the fastest rate of turn ($5°/sec^2$) produced both the fewest sensations of turning to the right during CW deceleration and the only vestibularly "correct" sensations of turning to the left immediately following the light period. Further, any feedback from the nystagmic reaction should have reinforced the occurrence of a primary sensation (turning to the left) since, upon darkening the room, the optokinetic response was quickly replaced by a left-beating nystagmus. Some observations made subsequent to these studies support this position. Subjects rotating at constant velocity in a totally dark room (nystagmus and turning sensations were no longer present) were exposed to a 1–3 sec period of room illumination. Several seconds after the lights were turned off, a clear turning sensation (in the true direction) was experienced. If decelerations in darkness were begun too soon after this period of room illumination, markedly long latencies of the vestibular turning sensation occurred.

There is considerable evidence which suggests that the subjective aspects of vestibular stimulation follow a different time-course than nystagmic reactions (e.g.[3,5,11]). The present data seem to support this view. Thus, following a period of room illumination, vestibular nystagmus recommenced almost immediately (although at an attenuated level), whereas the subjective response most often showed a reversal or was absent. However, the early onset and the markedly enhanced secondary subjective reactions following the visual stimulation, although they occurred at a different time, were similar to the effects produced on nystagmus and may have the same origin. That is, centrally integrated visual information appears to enhance an opposed vestibular process which probably arises as a result of "prolonged" stimulation. The fact that the subjective response frequently decays (sometimes terminating) during a prolonged stimulus, and shows only a brief post-stimulus reaction as compared with post-stimulus responses following stimuli of shorter durations seems to support this view.[6,9,11]

Some Additional Considerations. There is evidence which indicates that the occurrence of secondary nystagmus is related to duration of stimulation or to duration of the primary response.[1,14] However, a systematic exploration of stimulus rate-duration combinations has not been undertaken and it seems possible that acceleration rate may also be a factor (compare the occurrences of both nystagmic and subjective secondary reactions obtained here following $3°/sec^2$ stimuli for 20 sec with those following $10°/sec^2$ stimuli for 12 sec). In any event, it seems clear that at least certain kinds of visual stimulation can exert strong influences on secondary responses of both nystagmus and sensation. The kind of visual input which has been demonstrated as effective in this regard is that which makes available information about objects fixed with reference to the earth.[5,10] That is, the curtailment of primary nystagmus and primary sensations and most often some enhancement of secondary reactions occur as a result of either still-fixation on anchored objects or conflicting visual information regarding those same objects (optokinetic nystagmus or visual observations of the true direction of turn, both of which oppose the vestibular signals). Visual stimulation, of itself, does not appear sufficient to produce these effects, e.g., a target light which rotates with the subject does not obviate the turning sensation (although it reduces at least the amplitude of nystagmus). Further, Mowrer[13] noted that reversing normal vision and the normal direction of optokinetic nystagmus (with a prismatic pseudoscope) during rotation, so that the response was in the same direction as the vestibular reaction, had no effect on the duration or strength of the post-rotational nystagmus (comparisons were made with responses following the exclusion of vision during rotation). He did not report secondary effects but they were also unlikely to be observed since he examined all post-rotational responses in a lighted room. It appears that the element of conflict between vestibular and visual signals (and perhaps others of a sensory nature) is required to produce these alterations in the vestibular reaction (see also[10]).

V. Summary.

Visual information in conflict with vestibular signals was presented to groups of subjects by illuminating the test room for brief periods during angular deceleration, or immediately after termination of deceleration. Trials were otherwise in total darkness. Both primary nystagmus and primary subjective reactions were markedly shortened during the periods of darkness subsequent to the intervals of light. In addition, strong secondary reactions (nystagmic and subjective) frequently followed the vision-attenuated primary responses.

REFERENCES

1. Aschan, G. and Bergstedt, M.: The Genesis of Secondary Nystagmus Induced by Vestibular Stimuli. *Acta Soc. Med. Upsal.*, 60:113, 1955.

2. Brown, R. H. and Guedry, F. E.: Influence of Visual Stimulation on Habituation to Rotation. *J. gen. Psychol.*, 45:151, 1951.

3. Collins, W. E.: Task-Control of Arousal and the Effects of Repeated Unidirectional Angular Acceleration on Human Vestibular Responses. *Acta Otolaryng.*, Suppl. 190, 1964.

4. Collins, W. E.: Vestibular Responses from Figure Skaters. *Aerospace Med.*, 37:1098, 1966.

5. Collins, W. E.: Special Effects of Brief Periods of Visual Fixation on Nystagmus and Sensations of Turning. *Aerospace Med.*, 39:257, 1968.

6. Collins, W. E. and Guedry, F. E.: Duration of Angular Acceleration and Ocular Nystagmus from Cat and Man. I. Responses from the Lateral and the Vertical Canals to Two Stimulus Durations. *Acta Otolaryng.*, 64:373, 1967.

7. Dodge, R.: Adequacy of Reflex Compensatory Eye-Movements Including the Effects of Neural Rivalry and Competition. *J. exp. Psychol.*, 6:169, 1923.

8. Guedry, F. E.: The Effect of Visual Stimulation on the Duration of Post-Rotational Apparent Motion Effects. *J. gen. Psychol.*, 43:313, 1950.

9. Guedry, F. E. and Collins, W. E.: Duration of Angular Acceleration and Ocular Nystagmus from Cat and Man. II. Responses from the Lateral Canals to Varied Stimulus Durations. *Acta Otolaryng.*, 65: 257, 1968.

10. Guedry, F. E., Collins, W. E. and Sheffey, P. L.: Perceptual and Oculomotor Reactions to Interacting Visual and Vestibular Information. *Percept. Mot. Skills*, 12:307, 1961.

11. Guedry, F. E. and Lauver, L. S.: The Oculomotor and Subjective Aspects of the Vestibular Reaction During Prolonged Constant Angular Acceleration. *J. appl. Physiol*, 16:215, 1961.

12. Markaryan, S. S.: Vestibular Reactions Under the Effect of Various Angular Accelerations. In Parin, V. V. (Ed. in Chief) *Aviatsionnaya i Kosmicheskays Meditsina* (Aviation and Space Medicine), Akademiya Meditsinskikh Nauk, SSSR, Moscow, 1963. (NASA Technical Translation F–228, 1964, 305–308.)

13. Mowrer, O. H.: The Influence of Vision During Bodily Rotation Upon the Duration of Post-Rotational Vestibular Nystagmus. *Acta Otolaryng.*, 25:351, 1937.

14. Noto, A.: Studies on the Second Phase of Nystagmus. *J. Oto-, Rhino-Laryngol. Soc. Japan*, 63:40, 1960.

15. Ohm, J.: Uber den Einfluss des Sehens auf den vestibularen Drehnystagmus und Nachnystagmus. *Z. f. Hals-, Nasen-, u. Ohrenheilk.*, 16:521, 1926.

16. Preber, L.: Vegetative Reactions in Caloric and Rotatory Tests. *Acta Otolaryng.*, Suppl. 144, 1958.

17. Wendt, G. R.: Vestibular Function. In Stevens, S. S. (Ed.), *Handbook of Experimental Psychology.* Wiley & Sons, Inc., New York, 1951, 1191-1223.