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ADAPTATION TO VESTIBULAR DISORIENTATION.

VII. SPECIAL EFFECTS OF BRIEF PERIODS OF VISUAL FIXATION ON NYSTAGMUS AND SENSATIONS OF TURNING

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ADAPTATION TO VESTIBULAR DISORIENTATION

VII. Special Effects of Brief Periods of Visual Fixation on Nystagmus and Sensations of Turning[1]

1. The Problem.

In spite of daily exposure to strong angular accelerations, figure skaters show brisk vestibular nystagmus, experience motion, and can become disoriented when vestibular testing is conducted in the absence of visual information.[4] Even when ocular fixation on external objects is permitted, extremely brief periods of vertigo and blurred vision occur immediately following the skaters' high-velocity (up to 300 rpm) on-ice spins. The present study was undertaken to elucidate some of the mechanisms by which control of vestibular function is achieved through vision and to evaluate the effects of the skaters' experiences on their vestibular responses.

II. Method.

Subjects. Four male and four female skaters and four male and four female non-skaters were tested in the Stille-Werner RS–3 Rotation Device under identical conditions. Two practice trials were given in total darkness to familiarize the subjects with the test situation and to provide them with some practice in making subjective estimations of their acceleratory experiences.

Recording. Surface electrodes were taped by the outer canthi of the 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. RC time constants of 3-sec were used in amplification. Subjects were provided with a microswitch, connected to the recorder, by means of which signals indicating the subjective onset and termination of motion could be made.

Procedure. Subjects were seated in the rotation device with their heads upright but anteverted so that the lateral semicircular canals were approximately in the plane of rotation. They were instructed regarding the sequence of stimulus events and were given two familiarization trials.

Experimental trials comprised the following sequence:

1 & 2) "Dark" Trials: Acceleration 5°/sec² for 18 sec, 2 min constant velocity, deceleration 5°/sec² for 18 sec.

3 & 4) "Light" Trials: Acceleration 5°/sec² for 18 sec, 2 min constant velocity, deceleration 5°/sec² for 18 sec.

5 & 6) "Dark" Trials: Acceleration 15°/sec² for 6 sec, 2 min constant velocity, deceleration 15°/sec² for 6 sec.

7 & 8) "Light" Trials: Acceleration 15°/sec² for 6 sec, 2 min constant velocity, deceleration 15°/sec² for 6 sec.

9 & 10) "Dark" Trials: Acceleration 15°/sec² for 6 sec, 2 min constant velocity, deceleration 90°/sec² for 1 sec.

11 & 12) "Light" Trials: Acceleration 15°/sec² for 6 sec, 2 min constant velocity, deceleration 90°/sec² for 1 sec.

Half of the subjects in each group were given CW accelerations on odd-numbered trials and CCW accelerations on even-numbered trials; directions were reversed for the remaining subjects. "Dark" trials were conducted in total darkness. "Light" trials were also in total darkness with the exception of a 3-sec period (which began one sec after the termination of deceleration) when the room lights were turned on. During this period of illumination, subjects were instructed actively to fixate on the nearest to straight-ahead vision of a series of eye-level markers attached to the walls of the room. At the end of the 3-sec period, room lights were again turned off.

Scoring. Only deceleration responses were scored. Three measures were obtained for pri-

[1]Assistance rendered by Ruth Ann Mertens, Billy P. Updegraff, and David Schroeder is gratefully acknowledged.

mary nystagmus: duration, frequency, and slow-phase displacement. Duration was measured from the point at which the deceleration began to the last beat of the primary response. Frequency measures were obtain simply by counting the number of eye movements per 3-sec interval. Slow-phase displacement was calculated by measuring the vertical distance from the peak to the baseline of each nystagmic eye movement; these values were summed for 3-sec intervals and converted to degrees by means of calibration procedures employed prior to each trial. Measurement of secondary nystagmus was limited to the first 30 sec of response; thus, only slow-phase and frequency data were tabulated. Subjective reactions were examined from two points of view: latency (time from stimulus onset to first signal of experienced motion) and duration (time from stimulus onset to signal indicating end of experienced motion).

III. Results and Discussion.

Comparisons of Nystagmic Output. Mean slow-phase eye displacement, frequency of eye movements, and duration of primary nystagmus were tabulated independently for "dark" and "light" trials for skaters and non-skaters. These values appear in Table 1. For slow-phase and frequency measures, there is little difference between directions for skaters. For non-skaters, CW deceleration produced consistently more output than CCW stimulation, but this is entirely attributable to a single female subject who showed a marked directional preponderance of nystagmus. Duration data show no clear patterns of directional differences for either group of subjects.

The data for the two directions were combined and analyses of variance were performed. The analyses indicated that for primary nystagmus, the duration, the number of eye movements, and the total slow-phase displacement of the eyes were significantly greater ($p > .001$) for "dark" trials as compared with "light" trials for both skaters and non-skaters. Similarly, both groups of subjects showed significant differences in output ($p > .001$) for all three measures as a function of stimulus rate (although all three stimulus rates brought the subjects to a complete stop from 15 rpm, the 18 sec stimulus resulted in the greatest output of nystagmus).

In comparing skaters with non-skaters, the duration and frequency measures yielded no statistically reliable differences. However, non-skaters showed significantly greater ($p > .05$) slow-phase output compared with skaters for the three rates of stimulation.

The average nystagmic responses for each of the two groups of subjects were plotted in 3-sec intervals for the three stimulus rates. These plots of slow-phase displacement and frequency appear in Figures 1, 2, and 3. The greater slow-phase output for the non-skater group is evident

TABLE 1. Mean slow-phase eye displacement, number of eye movements, and duration of primary nystagmus for CW and CCW deceleratory stimuli for each trial and stimulus rate. The consistently greater output (slow-phase displacement and number of beats) to CW stimulation for non-skaters is attributable to a single subject with a marked directional preponderence.

			Slow-phase (Degrees)		*Number of Beats*		*Duration (Seconds)*	
Stimulus	*Subjects*	*Trial*	*CW*	*CCW*	*CW*	*CCW*	*CW*	*CCW*
5°/sec²	Skaters	Dark	744	841	84	93	50	56
		Light	482	493	63	67	42	39
	Non-Skaters	Dark	1099	1053	91	95	60	63
		Light	675	602	72	66	45	44
15°/sec²	Skaters	Dark	619	624	75	77	44	46
		Light	319	347	50	55	32	40
	Non-Skaters	Dark	948	871	82	76	49	47
		Light	545	516	65	60	32	33
90°/sec²	Skaters	Dark	625	624	71	74	42	42
		Light	262	258	40	41	25	29
	Non-Skaters	Dark	899	771	78	68	46	40
		Light	394	364	65	48	28	29

throughout the course of the response in each case. For frequency data, the skaters tend to have a number of eye movements equal to or greater than that of the non-skaters during the stimulus and for a few seconds thereafter on "dark" trials. A similar trend is evident during the stimulus of "light" trials but, as soon as the period of visual fixation is introduced, the skaters' average eye-movement frequency drops off a little more rapidly. The skaters may thus be demonstrating a somewhat greater ability than the non-skaters to influence vestibular nystagmus as a result of even so brief a period of visual fixation.

Secondary nystagmus was also plotted in Figures 1–3. Analyses of variance of total slow-phase displacement and total number of eye movements for the 30-sec period of scored activity yielded no statistically reliable difference between skaters and non-skaters, nor was the output of secondary nystagmus for this period of time related to the rate of the angular deceleration (and thus not to the amount of primary nystagmus). Relationships between primary and secondary nystagmus and between stimulus duration and magnitude of the secondary response have been demonstrated in other studies,[5,8] but for a different range of stimulus values.

Influence of Visual Fixation. As noted above, the introduction of the light and the opportunity for active visual fixation resulted in a significant shortening of the primary nystagmic response and a significant reduction in the primary slow-phase and frequency measures for both groups of subjects (see Figures 4, 5, and 6). The skaters appeared to demonstrate more rapid response decline during the period of darkness following visual fixation than did non-skaters. Coupled with these reductions was a significant increase ($p > .01$ for slow-phase; $p > .001$ for frequency) in the output of secondary nystagmus during "light" trials. In addition to being more pronounced, the secondary reaction appeared much earlier following the "light" period than it did during "dark" trials. Some striking examples of these effects are evident in the tracings presented in Figures 7, 8, and 9. The opportunity to see stationary visual objects also shortened the subjective after-sensation.

Secondary Nystagmus. A number of authors have expressed the view that secondary nystagmus is due to central rather than peripheral events.[1,14] In addition, Guedry, Cramer, and Koella[10] ascribed secondary subjective reactions to processes which developed to counteract primary subjective reactions. It is felt that the marked secondary responses obtained in this study following a brief period of active visual fixation may lend support to both of these views. The present data are interpreted as indications that secondary nystagmus is of central origin, that the secondary reaction is a process which opposes the primary (whether it is initiated to do so, or occurs as a consequence of some central imbalance produced by "prolonged" activity in one direction), and that visual information signalled during a period of active ocular fixation is centrally integrated and enhances this already on-going opposed process (under some conditions), thereby attenuating the primary response.

Subjective Responses. Latency and duration of subjective turning reactions were calculated in seconds for both acceleration and deceleration stimuli for the two directions of rotation. Data were combined for those stimuli which produced sensations in the same direction (e.g., CW acceleration and CCW deceleration for right-turning sensations). All latency scores (Table 2) were subjected to analysis of variance and yielded only one main effect: the higher stimulus rates produced shorter subjective latencies ($p > .01$). Duration data (Table 2) also yielded a significant effect for stimulus rate ($p > .01$) with the higher rates of angular acceleration producing shorter durations of turning sensations. In addition, skaters had significantly shorter durations of the subjective response ($p > .01$) than did non-skaters. For duration analyses, no test was made of dark deceleration scores versus those obtained when the light was introduced. This was due to the fact that on only one occasion (for a total of 6 sec) did any skater experience motion after the introduction of the light, whereas in 17 of the 48 cases, non-skaters experienced some further (although markedly reduced) sensation of motion after the light was turned off. Thus a clear difference in duration of sensation between skaters and non-skaters was evident even after introduction of the brief period of visual information.

TABLE 2. Mean latency (from stimulus onset to subject's first signal) and duration (from stimulus onset to subject's final signal) in seconds for subjective reactions to three rates of angular stimulation. Unless otherwise indicated, scores are means for appropriately combined acceleration and deceleration stimuli. R- and L- turns indicate the duration of the subject's turning sensation. D and L refer to "dark" and "light" trials, respectively. Latency scores were rounded to the nearest tenth of a second; duration scores to the nearest second.

		Skaters		*Non-Skaters*	
		R-turn	*L-turn*	*R-turn*	*L-turn*
Rate	*Trial*		*Latency*		
5°/sec²	D	2.4	2.4	2.8	2.3
	L	2.8	2.8	2.6	2.4
15°/sec²	D	1.1	1.1	1.2	1.2
	L	1.1	1.2	1.1	1.2
90°/sec²	*D	0.6	0.7	0.5	0.6
	*L	0.6	0.7	0.5	0.6
			Duration		
5°/sec²	D	30	30	36	36
	**L	30	28	33	34
15°/sec²	D	19	15	22	22
	**L	20	17	23	24
90°/sec²	*D	13	11	18	17
	*L	Insufficient Data		Insufficient Data	

*Means based on deceleration data only (acceleration rate was 15°/sec²).
**Means based on acceleration data only (see text).

Visual-Vestibular Interaction. The present data indicate that visual stimuli can exert a strong influence on the vestibular reactions of human subjects. Not only are primary nystagmic reactions markedly affected by even a brief opportunity to see stationary visual surroundings, but the intensity of the subjective reaction is either sharply reduced or the vestibular sensations are abruptly terminated. Further evidence for visual-vestibular effects has been presented in an earlier study of figure skaters[4] where it was noted that weak nystagmic responses were obtained when skaters were given opportunities to fixate visually during laboratory caloric stimulation, whereas eye closure or tests in total darkness resulted in vigorous responses. Similarly, the skaters demonstrated the learned ability to bring under rapid visual control, by fixating immediately on some object at the conclusion of a spin, the turning sensations and nystagmus which would have resulted from their abrupt on-ice decelerations.[4] When this practiced opportunity to use visual information to suppress actively the vestibular consequences of their quick stops from high-velocity spins was prevented by eye closure, brisk nystagmus, disorientation, staggering, loss of balance, and falling occurred. These findings appear to substantiate the view propounded by Wendt[11] who indicated that, "...visual stimuli tend to inhibit the vestibular nystagmus, and with repetition these stimuli become increasingly dominant. Such habituation is probably not preventable." However, based upon data obtained from the skaters, this learned control of vestibular responses appears to transfer only incompletely (e.g., reduced slow-phase eye excursion and shorter subjective reactions) to situations in which vision is not permitted. Wendt[14] also made note that strong nystagmus is obtained from human subjects in the absence of visual stimuli regardless of practice if subjects are kept alert.[2]

A Modified View of Habituation. Introduced by Abels in 1906, the term "habituation," signifying a response reduction, has been employed to describe the effects of repeated elicitation of vestibular nystagmus. The process has been defined as "a tendency merely to drop out responses."[12] However, it is felt that the term "habituation," with its implications of an overall depression of responses has limited applicability and does not convey adequately some of the processes which may be activated by repeated vestibular (and perhaps other) stimulation.

The results of this study appear to support findings obtained in an earlier investigation[2] and suggest that a somewhat different view be taken of vestibular "habituation" phenomena in humans. In the earlier study, ten subjects were each given a series of 200 angular accelerations in which only one direction of nystagmus was elicited (decelerations were sub-threshold). These trials were spaced evenly over a 10-day period and, on the days immediately preceding and immediately following this 10-day period of repeated practice, sets of pre- and post-tests were administered in which nystagmus was elicited in both directions. A comparison of the pre- and post-test nystagmic responses showed that, for both directions of nystagmus, the amount of slow-phase displacement of the eyes declined throughout the course of the post-test response. The number of eye movements, however, showed a striking increase during periods of stimulation (4.15°/sec² for 13 sec) and for a few seconds thereafter (although total frequency showed a

slight decline). This increased activity was somewhat greater for the "practiced" direction of nystagmus, but was clearly evident for both directions. Moreover, the alterations in the nystagmic response pattern were still present one month later, with no intervening trials. It should be noted that all of the tests were conducted in total darkness.

Similar findings may be adduced from the present study. For all three stimuli (in "dark" and "light" trials), the skaters ("practiced" subjects) showed less slow-phase displacement throughout the course of the responses than did the non-skaters ("unpracticed" subjects). However, for the "dark" trials the skaters showed a greater frequency of nystagmus during the stimulus period and usually for a few seconds thereafter. This combination of lower-amplitude, higher-frequency nystagmus during stimulation and immediately following it, seems to be a characteristic of the vestibular response pattern of alert human subjects after exposure to repeated simple angular stimulation. Similar results have been presented by Wendt[13] in depicting responses to repeated oscillatory motion and to repeated single turns of short arc.

"Habituation," then, when used to signify a simple dropping-out of responses, appears not to describe adequately the vestibular processes which appear as a result of repeated elicitation of nystagmus in alert humans (although response declines and overall response depression may be characteristics of repeated vestibular stimulation of at least some animals[6]). Rather, what occurs is a change in the form of the response. Thus, in studies which maintained subjects in states of alertness, a simple "dropping out of responses" did not occur even after many stimulations, whether rotatory or caloric.[2,3] The response, however, appeared to be modified and perhaps this neutral term "modification" most appropriately describes the result of repeated simple vestibular stimulation. The modification appears to consist of greater fast-phase activity during angular stimulation with a concomitant reduction in the slow-phase excursion of the eyes. The nystagmus also appears to be more regular and the response may be thus somewhat better "tuned" to the stimulus. The process, then, is not a simple reduction but a dynamic change. It is suggested that one of the mechanisms basic to this change may be the opposed central process evidenced by secondary nystagmus.

With more complex ("Coriolis") stimulation, a marked reduction of nystagmus has been reported as a result of repeated experience.[7,9,11] That this apparent "habituation" may also be considered a dynamic process, and of the same nature as that described above, is suggested by the fact that, for a period of time following the response modification occasioned by repeated head tilts during rotation, head tilts made in a static condition (absence of rotation) have resulted in a nystagmic response opposed in direction to that which would have occurred had that same head tilt been made while the subject was still rotating.[8,11]

IV. Summary.

Groups of professional figure skaters and non-skaters were given a series of CW and CCW laboratory angular accelerations. Subjects were stimulated (a) in total darkness, and (b) in total darkness with the exception of a 3-sec period of room illumination which commenced one sec after a complete stop had been reached. Deceleration rates of $5°/sec^2$, $15°/sec^2$, and $90°/sec^2$ were applied from turning velocities of 15 rpm. Skaters produced significantly less primary slow-phase eye displacement than did non-skaters, but the groups did not differ in number of eye movements nor in duration of nystagmus. Introduction of the visual still-fixation period significantly shortened primary nystagmus and produced an accentuated secondary nystagmus for both groups. The term "habituation" (a "dropping out" of responses), used to define the effects of repeated vestibular stimulation, does not appear to describe completely the active process of change evidenced in the nystagmic tracings presented in this and other studies. Durations of turning sensations were shorter for skaters than for non-skaters. For both groups the period of room illumination, allowing subjects actively to fixate on stationary visual objects, significantly shortened or abruptly terminated the subjective reaction.

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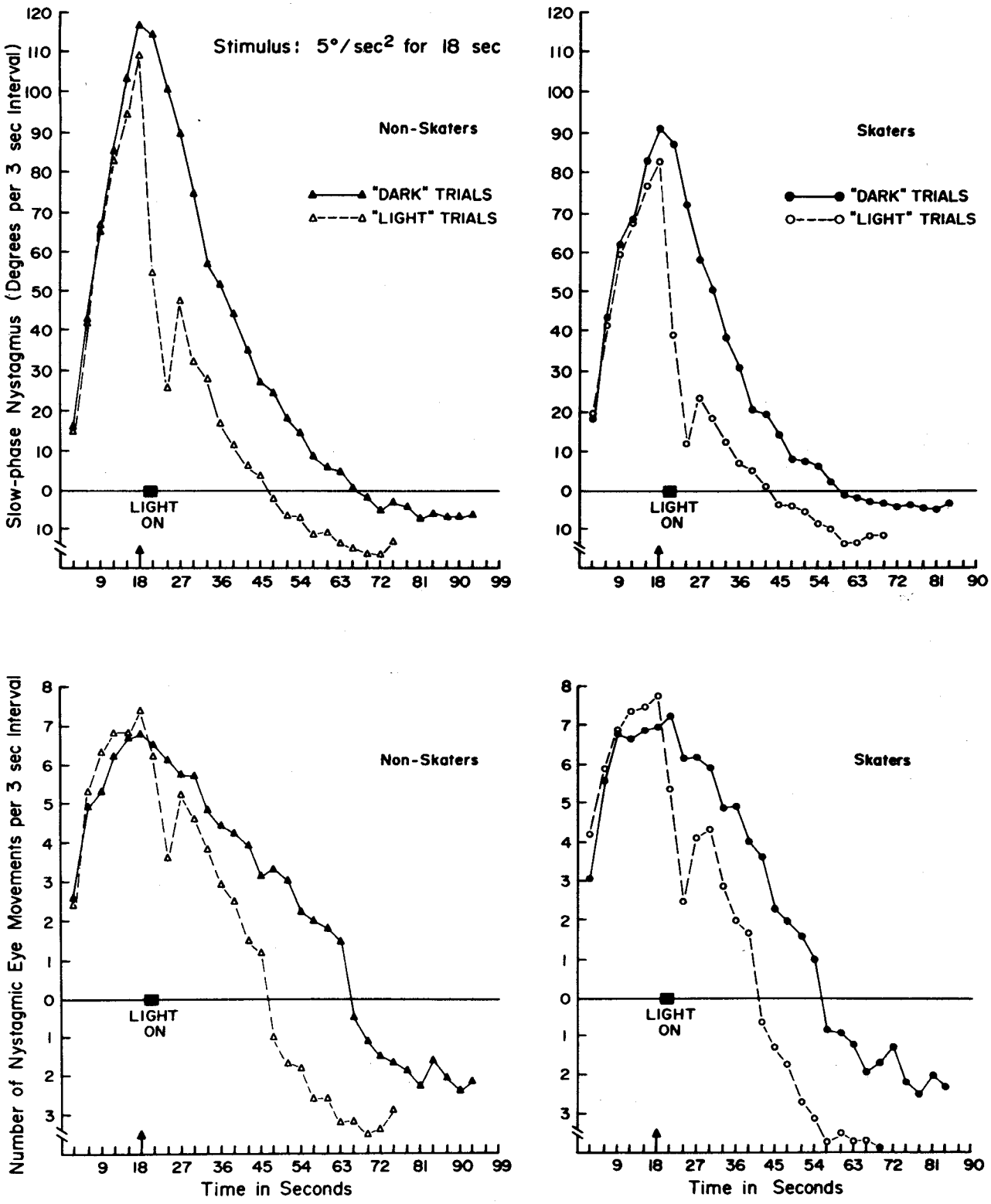

FIGURE 1. A comparison of the primary and secondary nystagmic output of figure skaters and non-skaters to "dark" and "light" trials using a 5°/sec² angular deceleration. Primary nystagmus plots are above, and secondary nystagmus plots below, the "0" line. Only 30 sec of secondary nystagmus was scored. Non-skaters show greater overall slow-phase displacement but less frequency of nystagmus during and shortly after the stimulus period in "dark" trials. Each point is an average for CW and CCW deceleration data for 8 subjects.

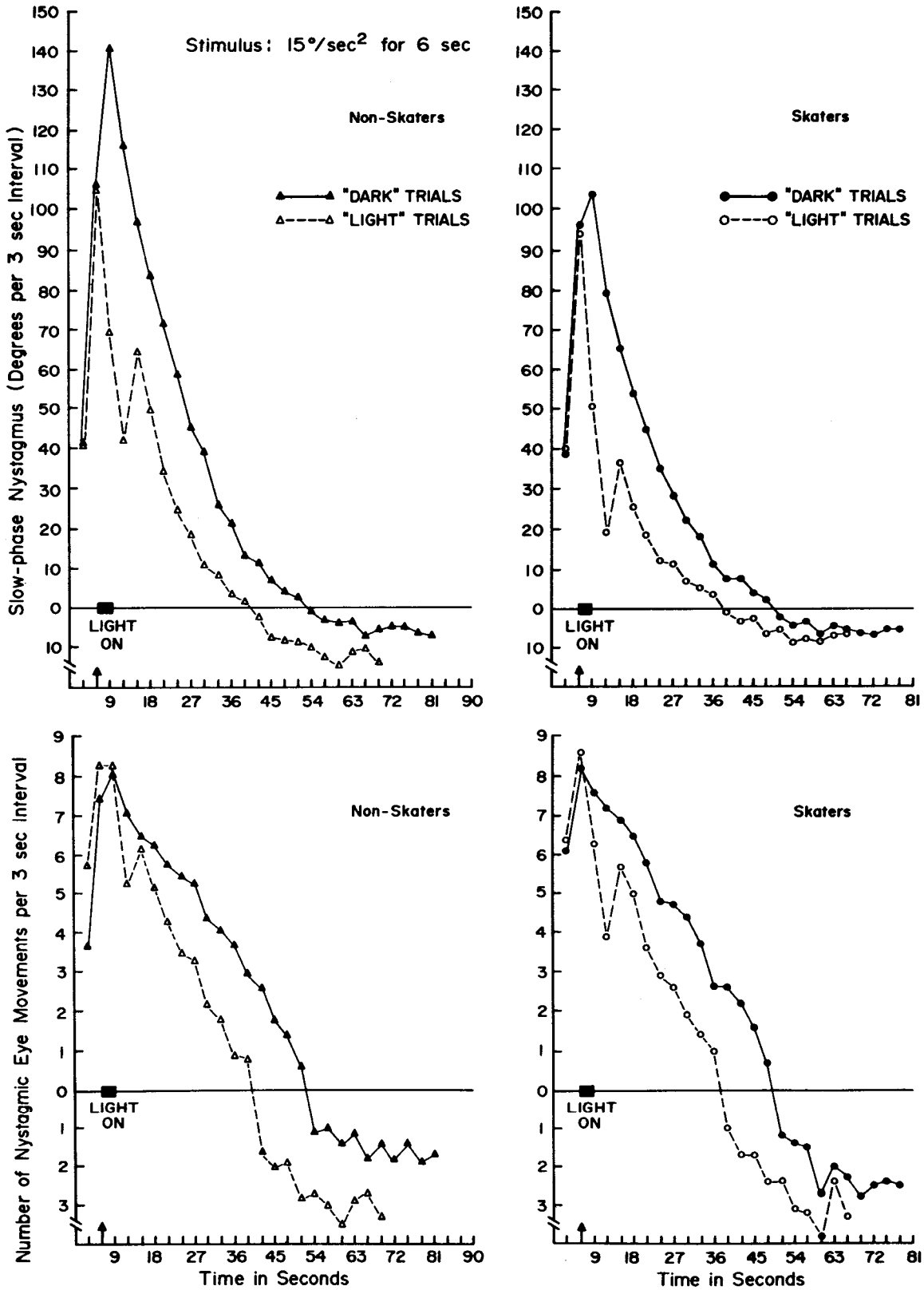

FIGURE 2. A comparison of the nystagmic output of figure skaters and non-skaters to a 15°/sec² angular deceleration. Compare with Figure 1. Note "overshooting" of nystagmus slow-phase measures for both groups during the "dark" trial to this brief stimulus (see Guedry & Collins[8]).

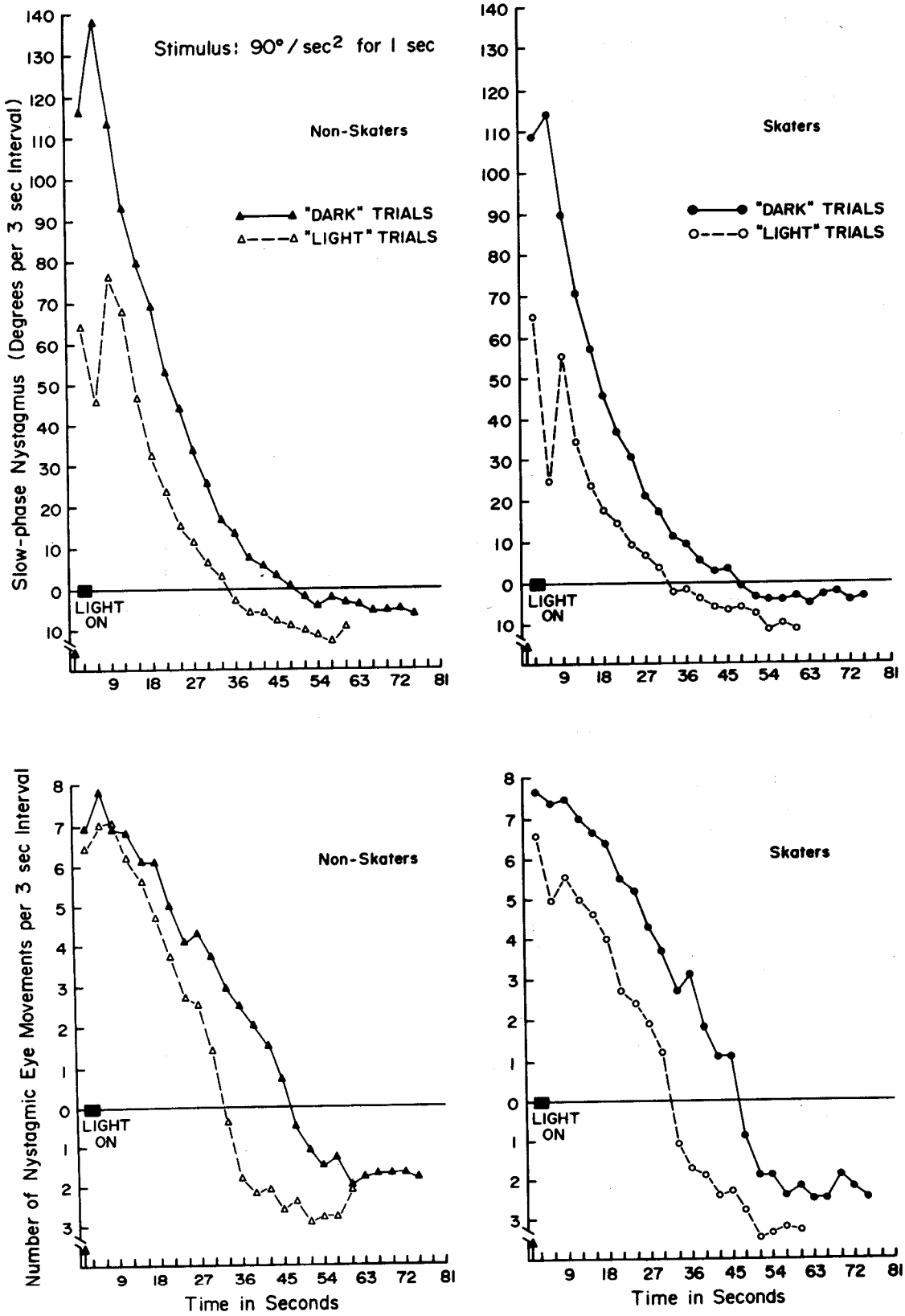

FIGURE 3. A comparison of the nystagmic output of figure skaters and non-skaters to a 90°/sec² angular deceleration. Compare with Figures 1 and 2.

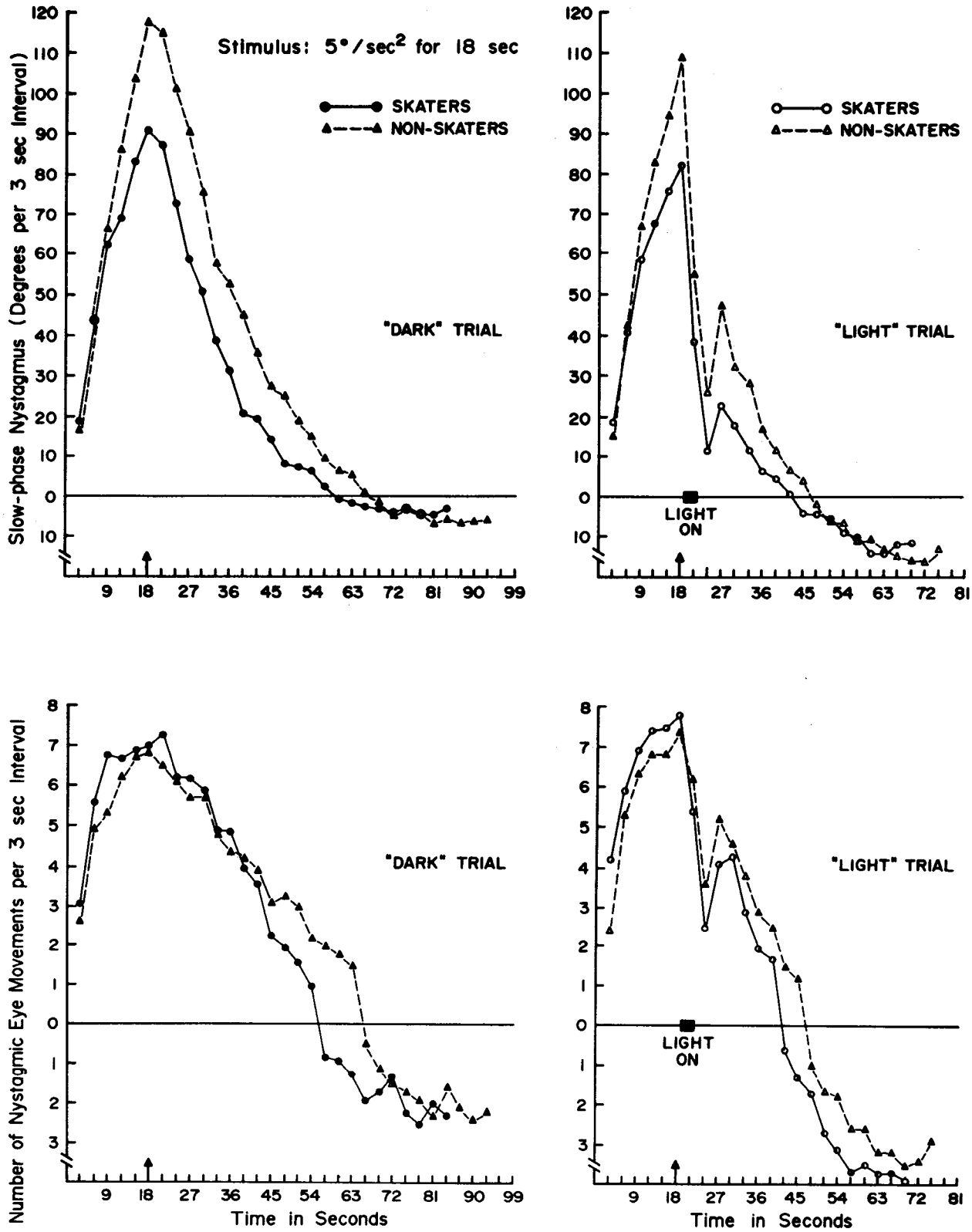

FIGURE 4. A comparison of nystagmic output to a 5°/sec² stimulus during "dark" and "light" trials for non-skaters and for figure skaters. Scoring and plots are the same as in Figure 1. Note the early onset and greater magnitude of secondary nystagmus during "light" trials.

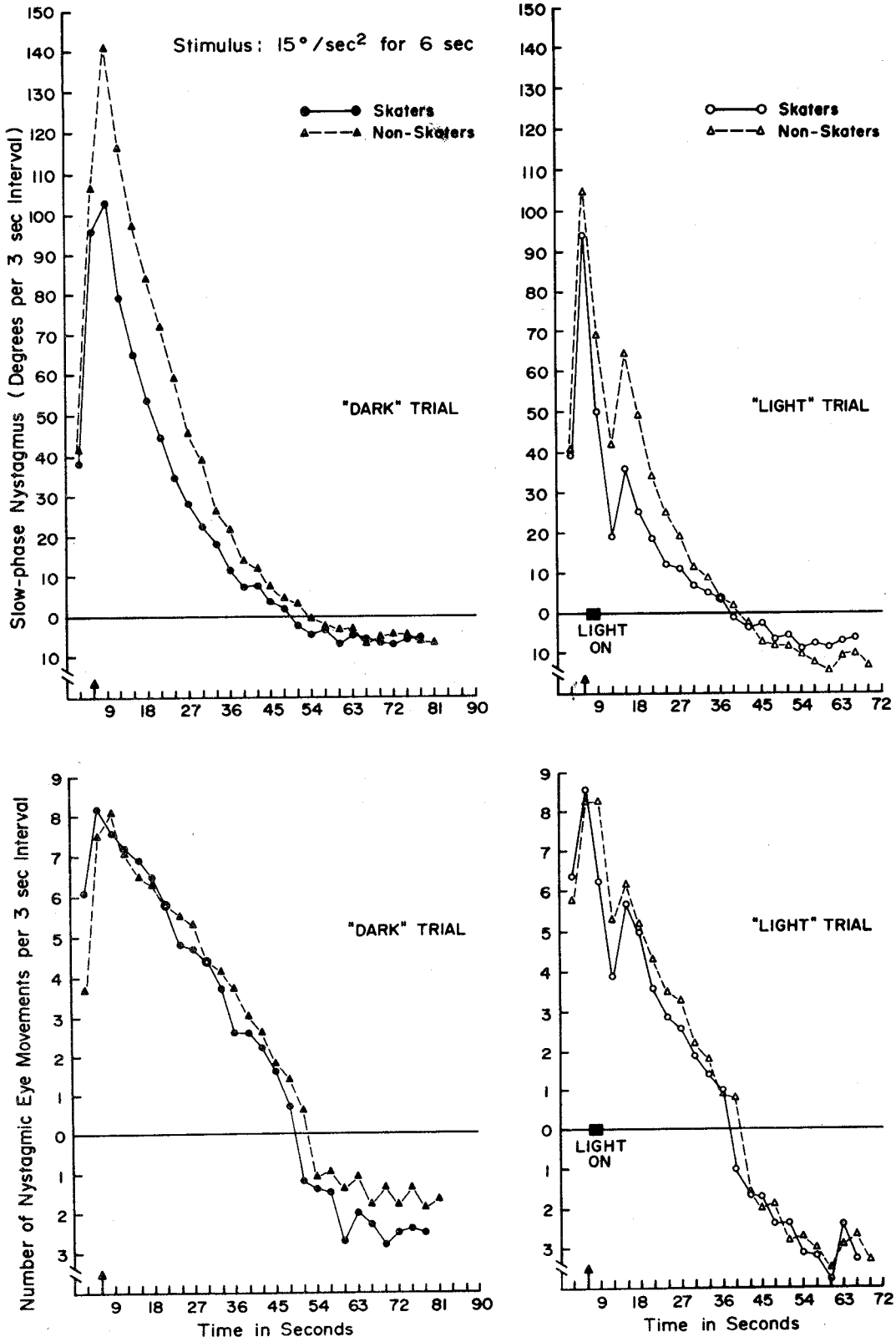

FIGURE 5. A comparison of nystagmic output to a 15°/sec² stimulus during "dark" and "light" trials for non-skaters and for figure skaters. Compare with Figure 4.

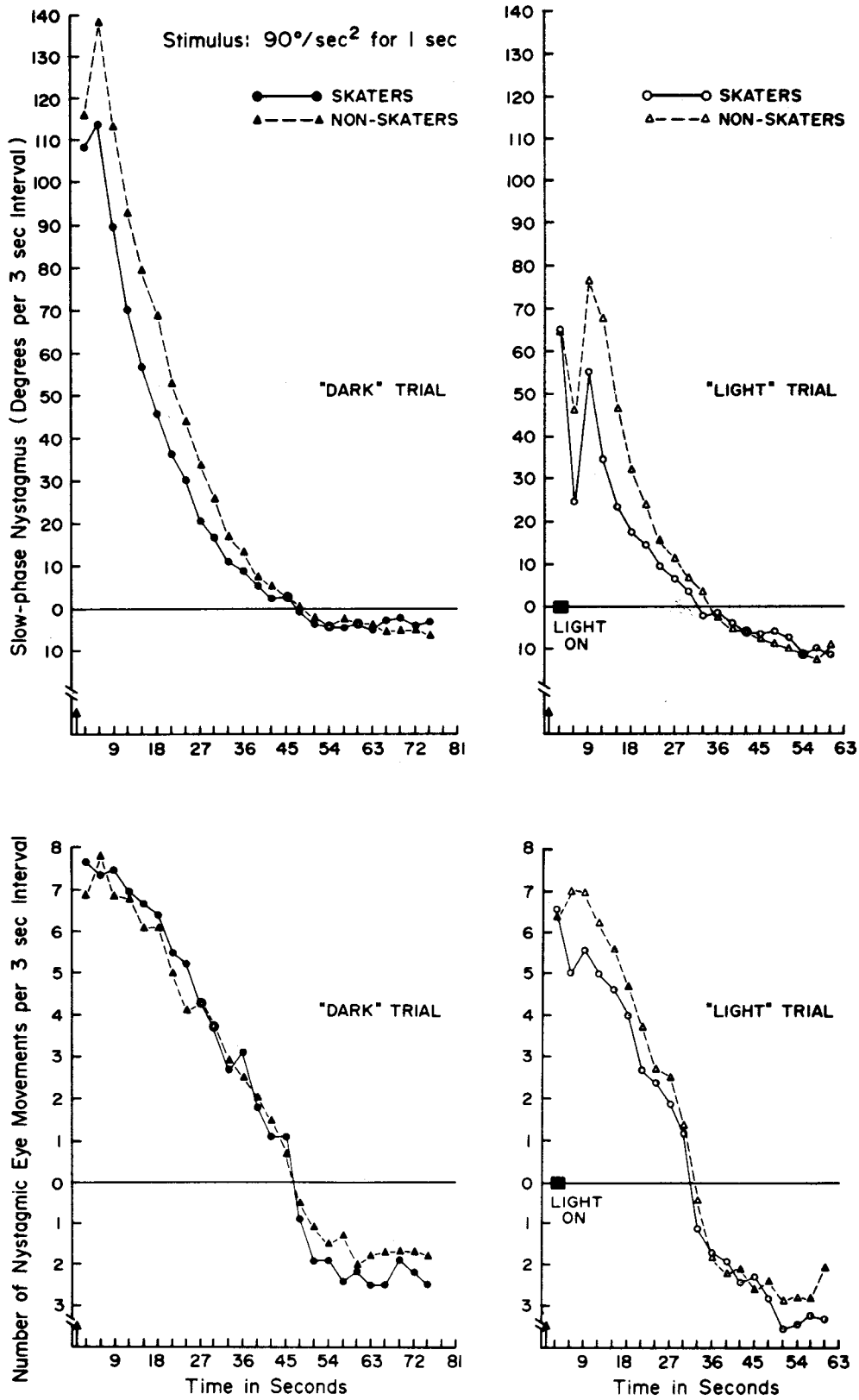

FIGURE 6. A comparison of nystagmic output to a 90°/sec² stimulus during "dark" and "light" trials for non-skaters and for figure skaters. Compare with Figures 4 and 5.

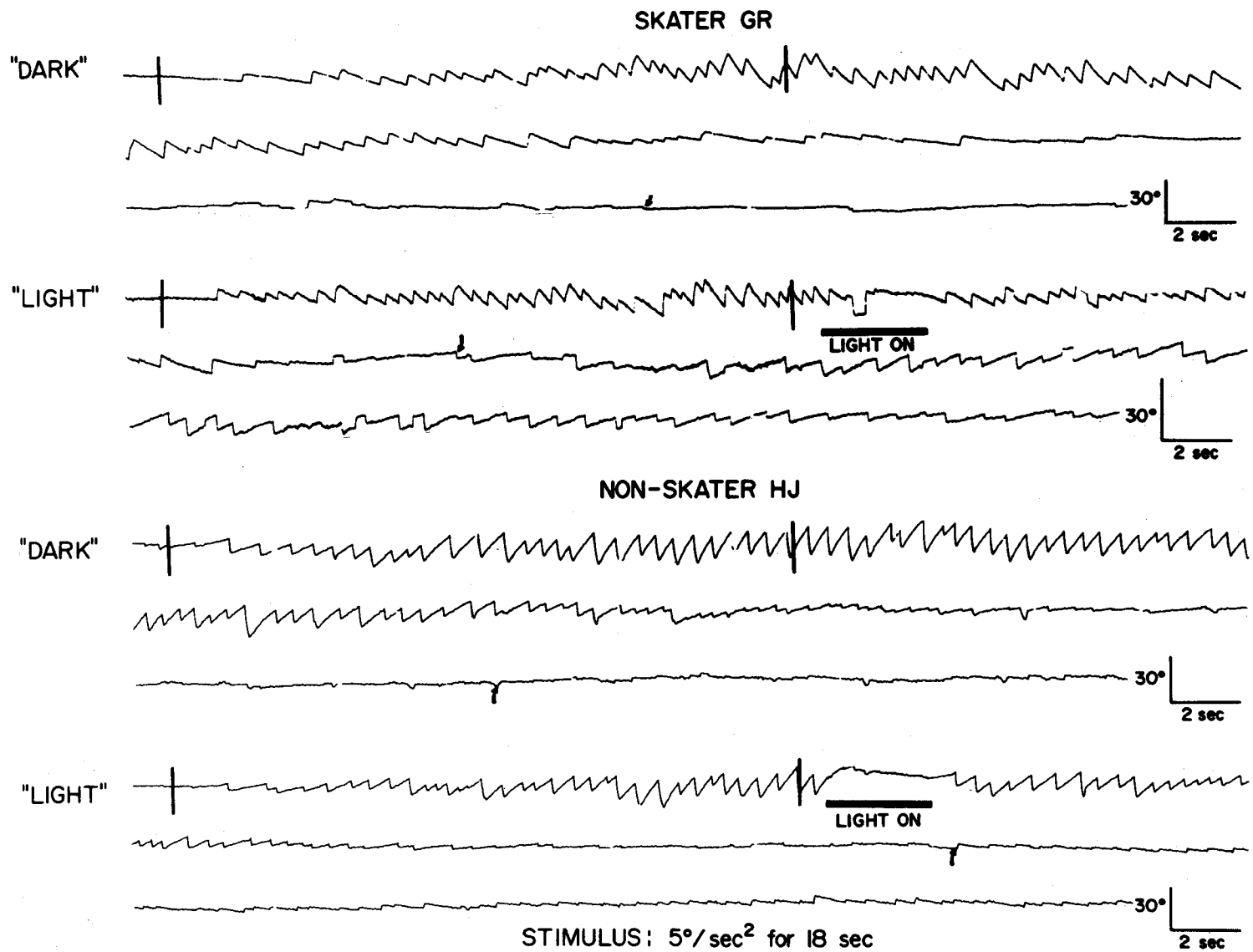

FIGURE 7. Tracings of nystagmus from a skater and a non-skater to a deceleration of 5°/sec² from 15 rpm (rotation was CCW for GR, CW for HJ). Both "dark" and "light" trials are presented. Tracings are continuous for each condition. Vertical bars through the tracings demarcate the stimulus periods. Arrows indicate the onset of secondary nystagmus. Note the greater vigor and the earlier onset of the secondary response during "light" trials.

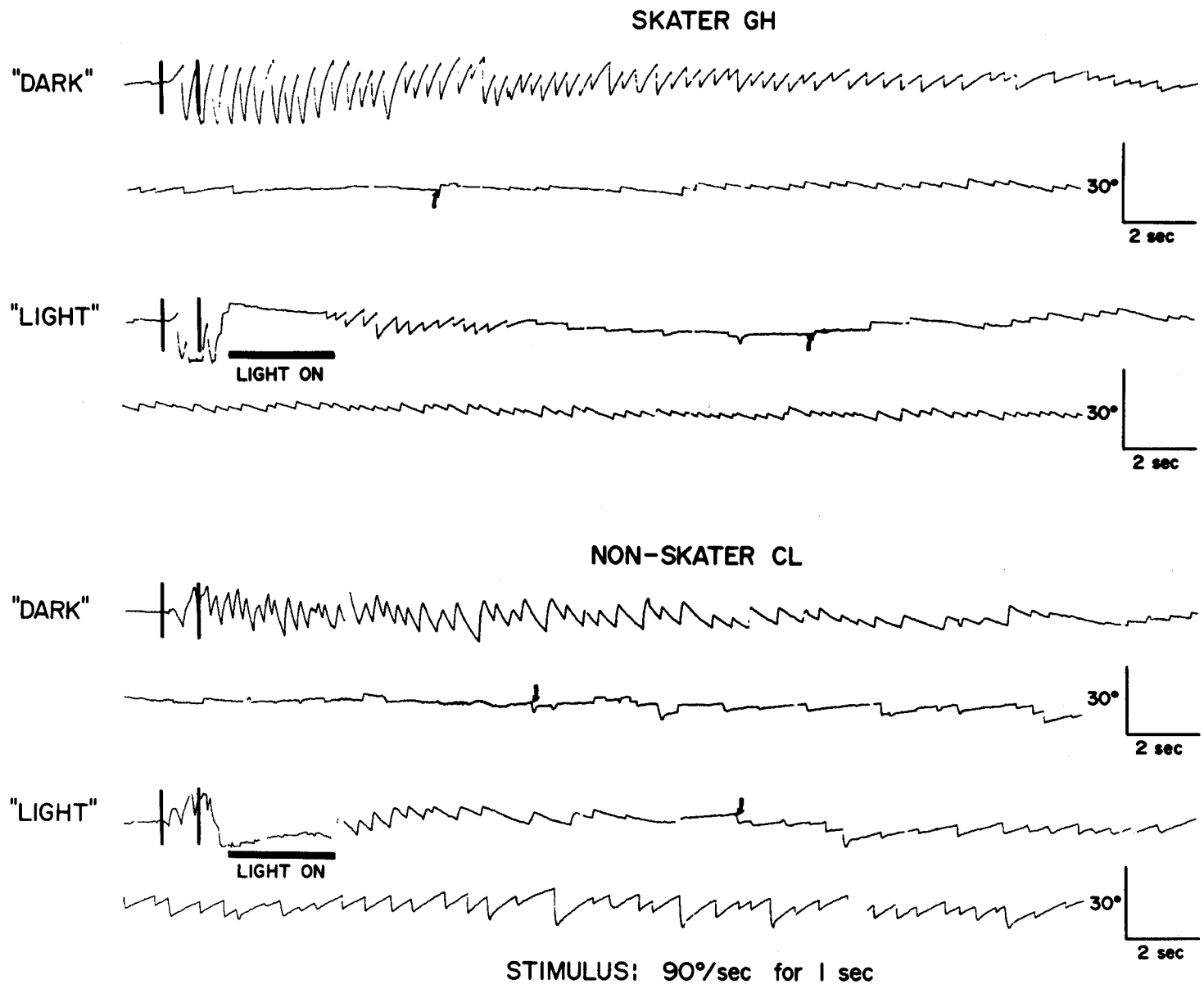

FIGURE 8. Electronystagmographic tracings from a skater and a non-skater to a deceleration of 90°/sec² from 15 rpm (rotation was CW for GH and CCW for CL). Markings are the same as in Figure 7.

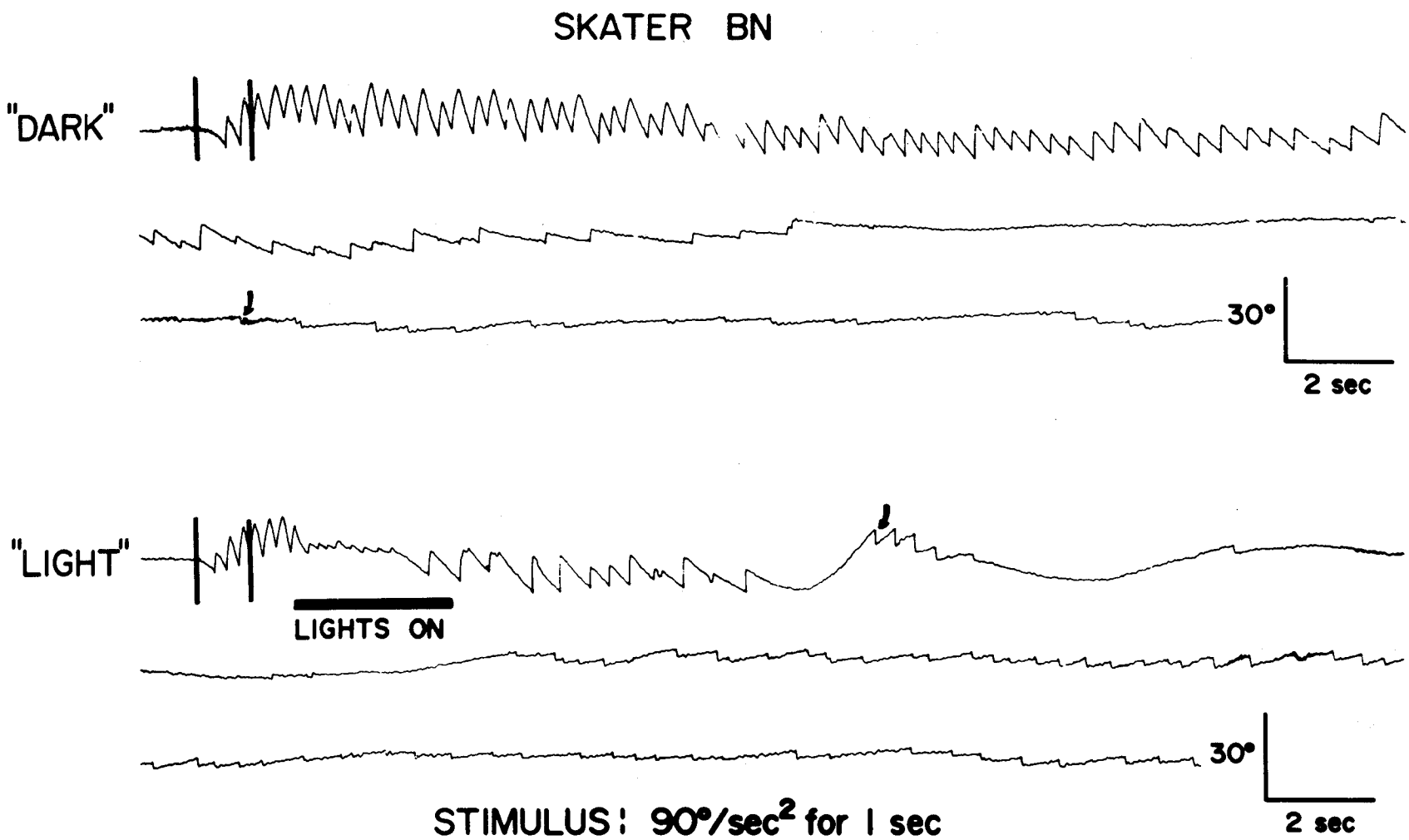

FIGURE 9. Primary nystagmus was interrupted by a secondary response particularly rapidly in this subject during the "light" trial. Markings are the same as in Figures 7 and 8.