

Audio-Ocular Response: Saccadic Programming

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The eye movements elicited by auditory stimuli—the audio-ocular response (AOR)—differ from those made in response to a visual target. The movements consist of both monosaccadic and multiple saccadic refixations (MSR). In visual refixation, monosaccadic refixations are always accurate; in AOR, they rarely are. In MSR, many strategies were used in the attempt to find the target but they were not always successful. However, final amplitudes of the total refixation were quite accurate in both MSR and monosaccadic refixations. Velocity profiles of the AOR showed such anomalies as discrete decelerations and multiple, closely-spaced saccades. These data suggest that, without visual feedback, the location of acoustic targets is difficult. In the absence of visual afference, when vigilance may be decreased by the lack of arousal, the velocity profiles also became abnormal, even at small amplitudes. Thus, for cockpit warning devices, a combination of auditory and visual indicators should be used.

IN PREVIOUS STUDIES, the latency, accuracy, and velocity characteristics of acoustically evoked saccades—the audio-ocular response (AOR)—were examined in human subjects (18–20). According to these investigations, the eye movements elicited by auditory stimuli were slightly less accurate and had longer latencies than those by visual stimuli. They were also slower (longer duration and smaller peak velocity) than visual saccades but faster than spontaneous saccades in darkness.

The strategy of coordinated eye-head movements elicited by auditory targets has also been investigated in monkeys. By strategy, we mean the way in which a refixation is programmed. Similar responses to auditory

and visual targets were found (15). These studies suggest the existence of a motor program which directs the gaze toward targets of interest and that this same program can be triggered by inputs from different receptors. The saccadic eye movement strategy elicited by visual targets has been investigated extensively in normal subjects (14) and in various pathological conditions: Eaton-Lambert syndrome, occipital hemianopsia, and in patients with myasthenia gravis (4,10,13). However, in view of the lack of information about the saccadic strategy to auditory targets, the present study was undertaken using our previously acquired data to examine whether elimination of visual input, the major ocular motor feedback path, alters saccadic programming or whether the way in which a refixation is made is solely a function of its amplitude. Such information not only interests neurophysiologists but also human factors engineers, and is of particular importance to designers of cockpit instrumentation. For example, how accurately and in what time frame can a pilot direct his gaze to an auditory warning in a cluster of instruments? Would either the accuracy or localization time improve if a visual stimulus were added?

METHODS

Eight subjects, ranging in age from 24–32 years, were studied. They were seated 1.14 m from an arc of the same radius, upon which were mounted light-emitting diodes at 5° intervals and loudspeakers at 0°, ±10° and ±20°. The loudspeakers were concealed from view by a screen at all times. Band-limited noise bursts (2 octaves wide, center frequency 1.5 kHz, intensity 85 db,

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duration 1 s) were used as the auditory stimuli. The recording area was in near-darkness.

Eye movements were recorded using a Narco Bio Systems Model-200 infrared system and a modified Beckman Type-R rectilinear Dynograph. The bandwidth of the entire system, position and velocity, was DC-100 Hz. Calibration was carried out using LED targets, which were subsequently turned off except for the 0 degree light, which served as the fixation point from which the sound-evoked saccades were made. Latency, accuracy, and velocity could be measured to 10 ms and 0.5° and $10^\circ \cdot s^{-1}$, respectively. Full details of the methodology may be found in Zahn *et al.* (18).

RESULTS

A total of 608 saccades for target eccentricities of 20° and 540 saccades for 10° targets were considered. The eye movements to the left and right of both eyes were summed, as no consistent difference was found between them.

Multiple saccadic and monosaccadic refixations: The eye movements of normal subjects to acoustic targets consisted of monosaccadic and multiple saccadic refixations (MSR). The frequencies of occurrence of both types of response are shown in Fig. 1.

In visual refixation saccades, monosaccadic refixations occur when the eyes bring a new part of the visual field to the foveal region with only one movement (orthometric). In AOR saccades, the monosaccadic refixations were orthometric (O) only a small percentage (11% for the 20° and 10.9% for 10° target refixations) of the time. If a saccade is not orthometric, it may fail to reach the target (hypometric-HO) or go beyond the target (hypermetric-HR). For 10° targets, there was a 36% incidence of HR saccades and a 53% incidence of HO saccades. For 20° targets HR saccades decreased to 28% and HO increased to 60%.

In saccades to a visual target, a second always corrective saccade is present when the initial one is inac-

curate. Second saccades occur in about 30% of 10° refixations and in about 57% of 20° refixations (14). As shown in Fig. 1, the AOR strategy consisted of MSR 60.4% of the time for target eccentricities of 20° and 47.4% for 10° . In 19.9% of 20° and 13.4% of 10° target steps, three or more saccades were present. Fig. 2 illustrates the ways in which refixations can be grouped, based on the relationship between their first and second saccades. In AOR, second saccades are corrective (orthometric) in only a few cases, as reported in Table I, group I. Third or fourth saccades, when present, are not always corrective. Unlike the visual saccades of normals, eye movements to auditory stimuli can exhibit large numbers of MSR and still not be on target at their termination. Another striking difference is that MSR following the first saccade are not always directed at the physical location of the target.

The amplitude of each individual saccade in an MSR varied randomly from one movement to another. Generally, the first saccade was the largest, consisting of approximately 75% of the final position of the refixation (Table II). In a few cases, the second saccade was larger than the first. A staircase movement, consisting of a series of step-wise saccadic movements, was occasionally present.

The intersaccadic intervals in MSR were usually short—approximately 130 ms—when a staircase movement was present (Fig. 1, col. 3). Less frequently, the latency of the second saccade was very long—greater than 500 ms—but usually normal for subsequent corrective saccades if they were present (Fig. 1, col. 4). Rarely, increased intersaccadic intervals of more than 350 msec between all corrective saccades or a normal latency of the second saccade and increased intersaccadic intervals between other corrective movements were seen.

The duration of MSR depended on both the number of saccades employed and the intersaccadic intervals. Most MSR took more than 500 ms—often 800 ms or

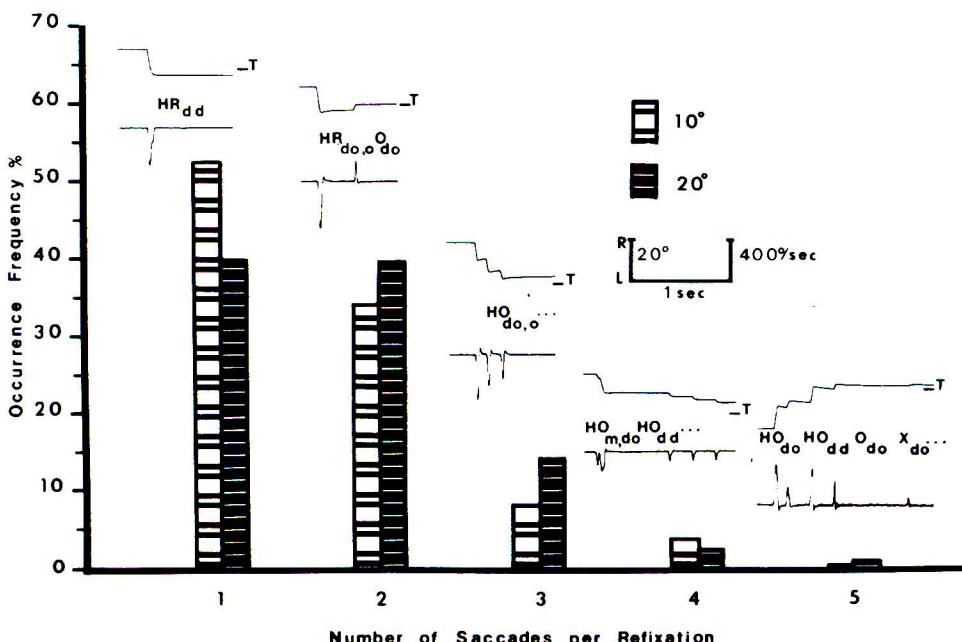


Fig. 1. Percentage of (1) monosaccadic and (2–5) multiple saccadic refixations (MSR) occurring for 10° and 20° targets. At the top, examples of monosaccadic and MSR are shown. Each example contains both a position (above) and velocity (below) eye movement tracing. HR = hypermetric, O = orthometric, HO = hypometric, do = dynamic overshoot, dd = discrete deceleration, m = multiple saccade, X = noncompensatory eye movement. For eye movement examples, R = right, L = left; position, velocity and time scales as shown.

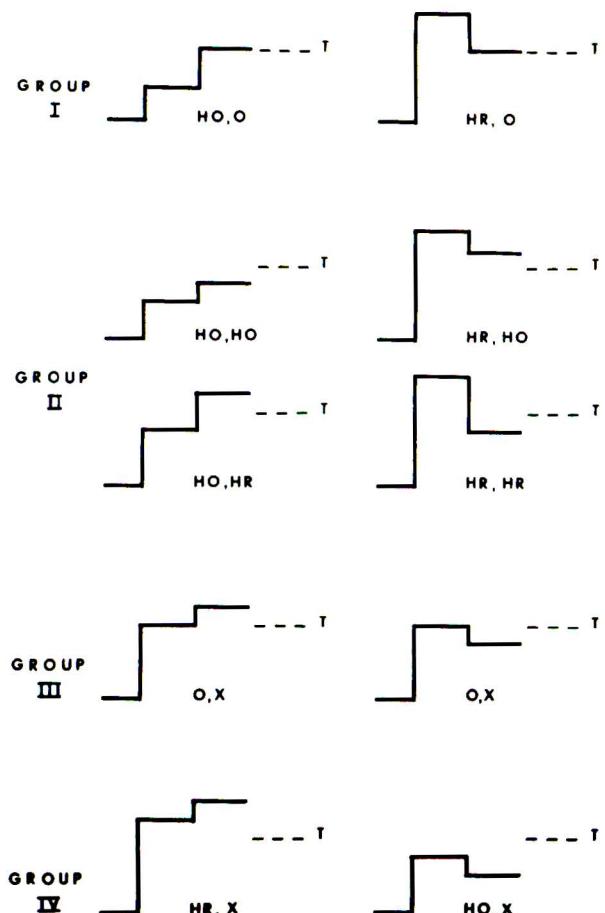


Fig. 2. An illustration of the metrics of MSR second saccades. I. This group is analogous to visual saccades (i.e. the second saccade is fully corrective). II. The second saccade is corrective in direction but not in amplitude. III. Unlike visual saccades, the second takes the eyes off target. IV. Again, unlike visual saccades, the second saccade takes the eyes farther from the target. O = orthometric, HO = hypometric, HR = hypermetric, and X = unrelated to metrics since eye was on target before this movement or this movement caused a larger error than had existed.

more—and sometimes were still in progress after the auditory stimulus ceased. The amplitudes of monosaccadic and multiple saccadic refixations were often different. Commonly occurring trajectories in MSR and monosaccadic refixations consisted of dynamic overshoots (do), dynamic overshoots with overshoot glissades (do,o), and glissadic overshoots (o). Details of this notation and the metrics notation used below may be found in Schmidt *et al.* (13). Combinations of these abbreviations may be used to describe complex movements.

Gains of MSR first saccades and of the single saccades: The gain (saccadic amplitude divided by target

TABLE I. PERCENTAGE OF RESPONSES OF GROUPS I-IV.

Groups	20°	10°
I. (HO,O; HR,O)	13.97	12.1
II. (HO,HO; HO,HR; HR,HO; HR,HR)	55.34	49.6
III. (O,X; O,X)	9.04	11.32
IV. (HR,X; HO,X)	21.64	26.95

amplitude) of the first saccade of MSR and of single saccades is reported in Table II. Single saccades showed a slight trend to undershoot 20° targets and to reach or overshoot 10° targets; they were quite accurate. Generally, the errors in the first saccades of MSR are greater than those for single saccades. Subject 7 showed a different pattern with more undershooting saccades for 10° targets (82% for single saccades and 100% for MSR) than 20° targets (36% for single saccades and 25% for MSR).

Final gain: The final gains of monosaccadic refixations and MSR (saccadic amplitude divided by target amplitude) are also reported in Table II. The data show a fairly large individual variation. In all the subjects (except subject 7) there is a trend to overshoot the target for saccades of 10°. A small trend to undershoot the target is present for saccades of 20° (subjects 1–5). Subject 6 was found to undershoot the target approximately 80% of the time, while subjects 7 and 8 overshot the target 53% and 51%, respectively.

Metrics of MSR second saccades: The movement following the initial saccade exhibited 10 distinct patterns, eight of which were not found in normal saccades to visual targets. Fig. 2 illustrates the possible combinations. We divided the 10 different patterns into four groups. In the first, the initial saccade was either hypermetric or hypometric and the corrective saccade was on target (orthometric); these two cases are analogous to visual saccades. In group II, an initial hypometric or hypermetric saccade was followed by a saccade which itself either undershot or overshot the target (HO,HO; HO,HR; HR,HO; HR,HR). For the third group, the initial saccade reached the target but the second saccade moved away from it (O,X; O,X). In group four, the inaccurate initial saccade was followed by a second saccade which increased the error of the first (HR,X; HO,X). The pattern described in the second group was most common in saccades to targets of both 10 and 20°, as shown in Table I.

Anomalous velocity profiles: The velocity profiles of saccades to visual targets for the amplitudes used in this study were smooth, narrow, and fairly symmetrical. In contrast, saccades to acoustic targets were more complex. Most striking were the discrete decelerations (dd), seen as abrupt halts in the velocity profiles, reflecting changes in the slopes of the saccadic trajectories. Another abnormality was multiple, closely-spaced saccades, (m) seen as two or more saccades spaced so closely together that their velocity profiles either overlapped or were closer together than normal corrective saccades. Fig. 3 shows the percentage of m and dd of both single saccades and first saccades of MSR made by all subjects for 10° and 20° amplitudes. This figure shows that the percentage of m and dd increased with refixation of 20° targets. Both m and dd were sometimes monocular phenomena. The same figure shows selected examples of anomalous velocity profiles. Such anomalies also existed in the later saccades of MSR.

DISCUSSION

Our recordings indicate that the saccadic eye movements elicited by auditory stimuli (AOR) employ a variety of strategies in the attempt to find the target. The

TABLE II. INITIAL AND FINAL GAINS OF AOR.

Subject	Gain of First Saccade of MSR		Gain of Single Saccades		Final Gain	
	20°	10°	20°	10°	20°	10°
1	0.86 ± 0.20	0.97 ± 0.25	0.93 ± 0.16	0.99 ± 0.40	0.93 ± 0.17	1.13 ± 0.38
2	0.70 ± 0.15	0.75 ± 0.30	0.95 ± 0.23	0.95 ± 0.44	0.93 ± 0.17	1.10 ± 0.35
3	0.76 ± 0.28	1.57 ± 0.47	0.80 ± 0.15	1.38 ± 0.66	0.84 ± 0.21	1.49 ± 0.46
4	0.83 ± 0.11	1.02 ± 0.34	0.84 ± 0.16	0.95 ± 0.61	0.88 ± 0.14	1.09 ± 0.44
5	0.75 ± 0.34	1.17 ± 0.30	0.93 ± 0.32	0.96 ± 0.52	0.93 ± 0.29	1.04 ± 0.40
6	0.57 ± 0.14	1.29 ± 0.48	0.70 ± 0.27	1.16 ± 0.63	0.65 ± 0.27	1.16 ± 0.62
7	0.94 ± 0.33	0.83 ± 0.33	1.03 ± 0.32	0.64 ± 0.31	1.03 ± 0.29	0.76 ± 0.30
8	0.91 ± 0.26	1.08 ± 0.52	0.96 ± 0.34	1.00 ± 0.32	1.03 ± 0.26	1.06 ± 0.42
Group	0.79	1.09	0.89	1.00	0.90	1.10

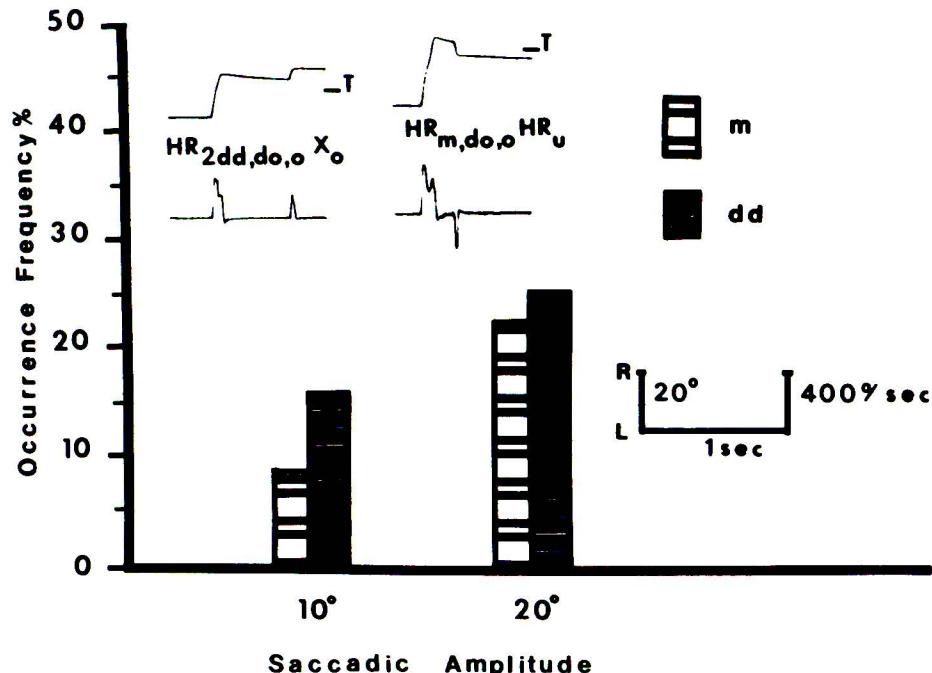


Fig. 3. Percentage of multiple, closely-spaced saccades (m) and discrete decelerations (dd) occurring for 10° and 20° targets. Selected examples of anomalous velocity profiles are shown. Each example contains both a position (above) and velocity (below) eye movement tracing. Eye position, velocity and time scales as shown for the eye movement tracings; R=right, L=left.

final amplitudes of the total movements were, however, quite accurate as shown by the final gain, although a large individual variation was present. The velocity profiles showed the presence of such anomalies as discrete decelerations (dd) and multiple, closely-spaced saccades (m).

Saccades to visual stimuli bring images of objects in the periphery of the visual field onto the fovea. Exactly how the ocular motor system directs these movements is the subject of various hypotheses. According to the retinotopic theory, the system operates on the basis of retinal input (11,17). The spatio-topic hypothesis holds that the system uses both retinal and extra-retinal eye position information and directs the eye to the spatial location of the target (8,9,12). Within the range of target steps of 10° and 20° used in this study, normal eye movements to visual targets would have either consisted of one orthometric saccade or two saccades where the second was always corrective.

Since the subjects had no visual information about the positions of the acoustic targets, they often searched for them with MSR. The first saccade, generally the largest, brought the eyes toward the target; the following saccade completed the search. This was an "open-loop" process, with the subject receiving no

sensory feedback about whether gaze angle was, in fact, becoming equal to the target angle.

In saccades to visual targets, if the initial refixation is inaccurate, the remaining error is almost always resolved by one corrective movement. When the MSR strategy is present in audio-ocular responses, only 13% of the second saccades reached the target for saccades of 20° and only 12% for 10° saccades. In other cases, the corrections were either in the wrong direction (group IV) or were not of the right size (group II). In a small percentage of the MSR, the first saccade was orthometric while the second saccade moved the eyes away from the target (group III). A third saccade—and sometimes more—was then used in an attempt to reach the target, raising the total refixation time to 500 ms or more compared to the 70 ms required for a normal orthometric 20° visual saccade. The protracted latencies of some second saccades (greater than 500 ms) may reflect a change in the perceived target location, requiring more processing time than a simple corrective saccade. Those MSR that continued after the cessation of the auditory stimulus differed from shorter ones because their final portions were directed by auditory memory rather than actual sensory input. It is likely that difficulty in locating the target was also the reason

why the latency of the first AOR saccade, as reported by Zahn *et al.* (18,19) and the intersaccadic intervals in MSR became longer compared with visual saccades. In order to have the same accuracy when estimating the target position, a longer acquisition time may be needed. Of course, our results show what subjects do in an artificial experimental situation with a fixed head position, and not necessarily what they do in their daily environment. Nevertheless, the wide variations in AOR saccadic programming contrast sharply with the more stereotyped visual saccades. This may indicate that the latter are related to a visible target and are not a simple function of refixation amplitude.

AOR saccades have been found to have such anomalies of velocity profiles as dd and m, which were not found in our recordings of visually elicited saccades at these amplitudes. Multiple closely spaced saccades can be elicited in monkeys by tracking a target whose velocity is instantly changed at varying intervals (3). Anomalies in the velocity profiles m and dd are also present in the primary saccades in the "anti-saccadic" task, where the subject is instructed to make an eye movement of equal and opposite magnitude to the stimulus step (7). In pathological situations, m and dd have been recorded in patients with myasthenia gravis (13) and the Eaton-Lambert syndrome (4). Fatigue is another putative cause of m (2). Both m and dd were found throughout our sessions, thereby making fatigue an unlikely explanation for their occurrence in this study. They have also been described in large-amplitude visual saccades (1) where no ocular motor fatigue was found.

It is difficult to explain exactly what common mechanism underlies the different occurrences of m and dd. It is likely that decreased performance in triggering the central motor program for saccades could be responsible for them in the anti-task test, in fatigued subjects, in monkeys that track a target with instantaneous changes in the velocity, and in AOR saccades. In large normal saccades and in those of myasthenics, they may represent a desynchronization of the neurons that generate the saccadic pulse.

It is likely that the superior colliculus (SC) is involved in controlling eye movements to various stimuli. Many cells here respond to visual, auditory, and somatic stimuli and the deep layers of the SC may contain superimposed topographic maps of the visual, auditory, and somatic fields (6). Projections from the striate cortex have also been shown in monkey (16). These may enhance the function of the SC in evoking eye movements to sound; in the cat's visual cortex, there are cells responsive to both visual and auditory stimuli (5). In our experiment, visual afference was not present, perhaps reducing arousal and causing the velocity profiles to become less synchronous. Another possible hypothesis is that, since the saccadic mechanism is specialized in foveating visual objects, its common function, it is less capable of bringing the fovea to other kinds of targets (rarely required).

In summary, AOR saccades exhibited different strategies and anomalous velocity profiles, indicating a relationship between the characteristics of the ocular

motor refixation and the stimuli which elicit them. Although overall accuracy was good, the variability and prolonged duration of these refixations suggest strongly that, where response time to an indicator is critical, i.e. in the cockpit, a combination of auditory and visual stimuli are required.

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