

Kinematics of Eye Movements of Cats to Broadband Acoustic Targets

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Populin, Luis C. and Tom C. T. Yin. Kinematics of eye movements of cats to broadband acoustic targets. *J. Neurophysiol.* 82: 955–962, 1999. Operant conditioning was used to train cats with their heads immobilized to localize sound by directing their eyes to the location of the sources. The kinematics of those eye movements were studied and compared with eye movements to visual targets at the same locations. The main finding of this study is that eye movements to broadband long-duration acoustic targets have two components: an initial slow phase of variable duration and a fast, normal saccade. The slow component is characterized by a persistent, shallow velocity ramp, while the saccadic component of the response falls on the main sequence computed from eye movements to visual targets. The slow component was shorter before saccades to long-duration stimuli performed under the delayed-saccade task and practically absent before saccades to transient acoustic stimuli. The results suggest that the initial slow component is used by cats to deal with uncertainty associated with the location of long-duration broadband targets and that the input to the saccade integrator(s) is similar under both visual and acoustic conditions.

INTRODUCTION

Eye movements of cats to visual targets are characterized by a sharp accelerating initial segment of roughly constant duration (Evinger and Fuchs 1978), typical of saccadic responses in other species (Baloh et al. 1975; Fuchs 1967; Hyde 1959). The larger the angular distance moved, the higher the maximal velocity achieved (Bahill et al. 1975; Boghen et al. 1974). This relation between maximal eye velocity and movement amplitude is roughly linear in cats (Evinger and Fuchs 1978), but in primates the function saturates for saccades larger than $\sim 20^\circ$ (Bahill et al. 1975; Fuchs 1967). A plot of this relationship, known as the main sequence (Bahill et al. 1975; Boghen et al. 1974), is a standard tool for determining if an eye movement falls in the category of saccades.

When the triggering signal for a saccade is nonvisual, such as an acoustic target, a direct effect on the dynamics has been reported in the form of a slower peak velocity (Engelken and Stevens 1989; Russo and Bruce 1994; Zahn et al. 1978; Zambambieri et al. 1982). However, the data are not in full agreement as Whittington et al. (1981) reported no differences between the kinematics of saccades to visual and auditory targets in monkeys.

Anticipatory eye movements have been observed before smooth pursuit of a moving target (Becker and Fuchs 1985; Boman and Hotson 1988; Kowler and Steinman 1979a) and

before saccades evoked by target steps of predictable direction (Kowler and Steinman 1979b; Moschner et al. 1996). Eye movements of this type required a retinal signal, did not result from attention shifts or practice, and could not be suppressed voluntarily. Although with lower frequency, such movements also were observed under conditions in which the amplitude and time of onset of the step were randomized (Kowler and Steinman 1979b).

Here we report an unusual type of eye movement in cats characterized by a slow velocity ramp that consistently preceded saccades to the location of long-duration, broadband noise targets. This eye movement is observed consistently under the standard-saccade conditions used in our sound localization studies (Populin and Yin 1998), unaffected by practice, shortened by delaying the execution of the response, and absent in responses to transient auditory stimuli. When the slow velocity ramp is removed from the eye movement records, the remaining quick component resembles a normal saccadic eye movement. The slopes of the regression lines fit to the main sequences of saccades to acoustic targets are similar to that of the saccades to visual targets. These results suggest that the initial slow component reflects the uncertainty associated with the location of long-duration broadband targets.

METHODS

General

A detailed description of the methods and training procedures is found in Populin and Yin (1998). Briefly, under sterile surgery we implanted cats with a small stainless steel head post modified from May et al. (1991) and eye coils (Judge et al. 1980) to measure eye position with the magnetic search coil technique (Robinson 1963). During experimental sessions, the cats were placed in a canvas bag and their heads restrained with a bar, modified from McHaffie and Stein (1983), attached to the head post from behind. The experiments were conducted in a dimly illuminated, sound-attenuated chamber with sound-absorbent foam covering the inner walls and major pieces of equipment.

Stimuli and eye-movement recordings

Acoustic stimuli consisted of long-duration (500–1,200 ms), broadband (0.1–25 kHz) noise bursts and single (100 μ s) clicks presented from any one of 15 speakers positioned 62 cm away from the center of the cat's head, along arcs in the horizontal or median sagittal plane, within the cat's oculomotor range ($\pm 25^\circ$) (Guitton et al. 1984). Visual stimuli consisted of red light-emitting diodes (LEDs) attached to the center of the speakers. The size of the speakers dictated a minimal separation of 9° between LEDs, which restricted the spacing and range of saccade amplitudes studied. In addition, cats rarely made

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saccades greater than $\sim 15^\circ$ to acoustic targets due to undershooting the target (Populin and Yin 1998). The speaker/LED assemblies were behind a black cheesecloth curtain that allowed the LEDs to be seen when lit and sounds to be heard. The position of the targets was specified with reference to the primary position ($0^\circ, 0^\circ$) defined as the point at eye level on the midline directly in front of the cat, with positive angles to the right or upward.

The analogue output of the coil system (CNC Engineering, Seattle, WA) was digitally sampled at 500 Hz with a 12-bit A/D converter. The experimental setup, including stimulus presentation and data collection, was controlled with a MicroVAX2 (Digital Equipment, Maynard, MA) computer running custom software.

Experimental sessions and tasks

The cats were trained using operant conditioning to look at the location of acoustic stimuli with their heads fixed. The experimental sessions consisted of a mixture of various tasks (fixations, standard and delayed-saccades, and sensory probes to visual and auditory stimuli) presented in random order from any of the speaker/LED assemblies so that the cat could not predict the type or the position of the upcoming target (Populin and Yin 1998). The length of each experimental session was primarily determined by the cat's willingness to participate. Typically sessions ranged between 3 and 5 h and included ~ 500 trials per day.

The standard-saccade task was used with two stimuli, the long duration noise and transient click stimuli. It began with a fixation LED presented at the primary position that the cat had to look at for 500–1,500 ms. Coinciding with the offset of the LED, an auditory or visual target was presented at a different location within the cat's oculomotor range. The duration of the long-duration stimuli was measured from the time the eyes entered the acceptance window set around the target.

The delayed-saccade also started with a fixation LED presented at the primary position, but its offset, which signaled the cat to make a saccade to the target, was delayed (300–700 ms) with respect to the presentation of the target. Only long-duration stimuli were used with this task.

Square electronic acceptance windows were set around the targets to provide a spatial margin of error: $2\text{--}5^\circ$ for visual targets and $6\text{--}12^\circ$ for acoustic targets. Larger windows were used for acoustic targets because the cats made larger errors in looking at these targets. For a discussion of the rationale for selecting the size of the windows, see Populin and Yin (1998). In both the standard- and delayed-saccade tasks, the cats were required to make a saccade to the target within 1,500 ms after the offset of the fixation LED. A food reward was delivered at the end of each trial in which the temporal and spatial criteria were met.

Data analyses—criteria to determine the start and end of the eye movements

Analyses were conducted off-line with custom graphics software that displayed horizontal and vertical eye position, several time derivatives of eye position, and other parameters used for data analyses. Eye position signals were smoothed digitally with a 5- to 11-point moving window average. Velocity was computed at each point using a first-order least squares fit on successive five-point windows. The procedure was repeated to compute higher-order derivatives. Although we designed the data analysis to be objective, we still found it necessary in $<5\%$ of the cases to intervene and override the points chosen by the program, usually due to noise artifacts.

Two events, the end of fixation and return to fixation, were computed from the time at which eye velocity departed from

and returned to, respectively, within 2 SD of its mean baseline. The mean baseline was computed from the velocity trace during the time interval comprising 100 ms before to 30 ms after the onset of the stimulus, during which time the eye was expected to be stationary. The eye position at the time of these two events defined the start and end of the saccade (Fig. 3 in Populin and Yin 1998).

RESULTS

The kinematic analyses that follow were carried out to quantify differences in cat eye movements to acoustic and visual targets. Most of the data presented in this report were recorded during the sound localization experiments presented previously and were selected from experimental sessions that had a large number of trials in the conditions of interest (Populin and Yin 1998). Because we did not screen these data in any other way, they are representative but only a small fraction of the entire set. Only trials that met the temporal and spatial criteria for success were analyzed. The percent of successes ranged between 65 and 88% for the standard-saccade task with long-duration stimuli, between 60 and 68% with transient stimuli, and between 35 and 80% for the delayed-saccade task. Most errors in the delayed-saccade task were early saccades due to anticipation, whereas most errors in the transient condition were due to a lack of response.

The difference between eye movements to long-duration visual and acoustic targets is illustrated in Fig. 1. Horizontal eye position signals (Fig. 1, *A* and *B*) and their corresponding velocities (Fig. 1, *C* and *D*) are plotted as a function of time. These data are a subset from Fig. 4 in Populin and Yin (1998), but here plotted synchronized to the end of fixation as defined in the methods section.

The initial segment of the eye movements was different in the two conditions. Visual trials (Fig. 1, *A* and *C*) were highly stereotyped: the eye started to move immediately in the direction of the target after the end of fixation with a high acceleration phase of uniform duration. In acoustic trials, on the other hand, the eye started to move in the direction of the target with a slow velocity ramp of irregular duration that preceded the fast saccadic component of the response (Fig. 1*D*). The presence of the slow velocity ramp in acoustic trials is illustrated more clearly in the insets of Fig. 1, *C* and *D*, which show magnified views of the velocity traces. Thus in visual trials the saccade coincides with the end of fixation criterion, but in acoustic trials it is preceded by a slow velocity ramp.

Saccade onset

The presence of the slow component in the initial part of the response to long-duration acoustic targets led us to seek an additional criterion that could objectively distinguish between the end of fixation and saccade onset in those eye movements with the slow velocity ramp. When applied to visual trials, which appeared to lack the slow ramp, the new criterion should mark saccade onset nearly coincident with the end of fixation. The irregular profile and the variable duration of the slow velocity ramp (Fig. 1*D*) precluded us from using a criterion based on a predetermined velocity threshold.

Empirically we determined that the first and fourth prominent peaks in the fourth derivative of position could be used as

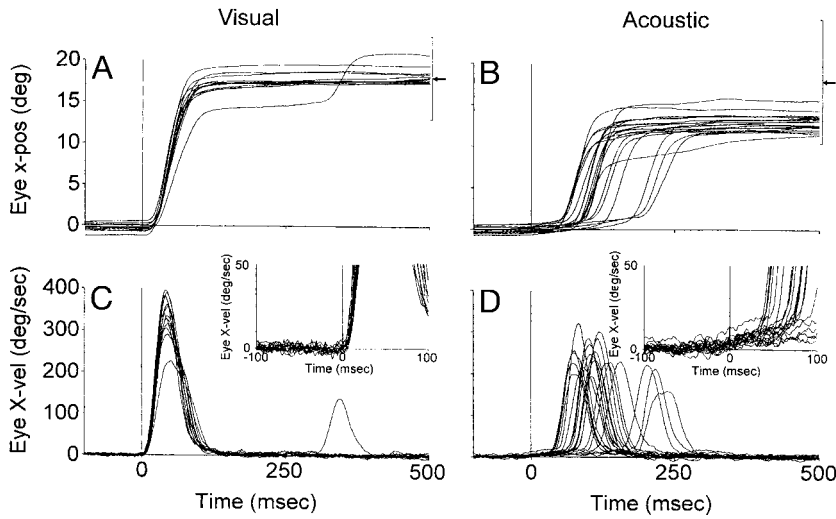


FIG. 1. Horizontal eye movement traces to visual (A) and acoustic (B) targets located at (18°, 0°) are plotted synchronized to the end of fixation at time 0 ms. ←, location of the target; |, size of the acceptance window surrounding the target. C and D: velocity of the position traces in A and B, respectively. Insets: magnified views of the velocity traces 100 ms before to 100 ms after the end of fixation. To visual targets, the eye moves sharply in the direction of the target immediately after the end of fixation. For acoustic targets, the saccadic response is preceded by a slow velocity ramp of variable duration.

markers for the onset and offset of a saccadic eye movement. Figure 2 compares this criterion to the end of fixation applied to both visual (top) and acoustic (bottom) trials. Both examples are saccades from the primary position to targets located at (-18°, 0°). If we define the start and the end of the saccade as the time of the first and fourth prominent peaks, respectively, in the fourth derivative (vertical dashed lines), then in the visual trial (Fig. 2, top) the end of fixation (vertical dotted line) and the saccade onset (vertical dashed line) occur nearly simultaneously, although saccade offset and the return to fixation do not. In the acoustic trial, on the other hand, saccade onset occurred almost 100 ms after the end of fixation (Fig. 2,

bottom). Thus in this visual trial saccade onset is essentially equivalent to the end of fixation, and we used it as an objective criterion for marking saccade onset in both visual and auditory trials.

Duration of the slow velocity ramp

We defined the duration of the slow component as the time elapsed between the end of fixation and saccade onset. Representative distributions of this measure for acoustic and visual trials to horizontal and vertical targets are illustrated in Fig. 3. In all five cats studied, the distributions of the duration of the slow component from visual trials are narrow (Fig. 3) with a mean near zero (Table 1), although the vertical trials had a broader distribution and correspondingly larger means, especially for cat 09, which confirms that for visual targets there was essentially no slow component. On the contrary, the distributions from acoustic trials to both horizontal and vertical targets are broader (Fig. 3) and have significantly larger positive means and larger standard deviations (2-tailed *t*-test, *P* < 0.01) (Snedecor and Cochran 1980), reflecting the presence of the slow velocity ramp. Thus saccades to acoustic targets are preceded by a slow velocity ramp that is generally not present in saccades to visual targets.

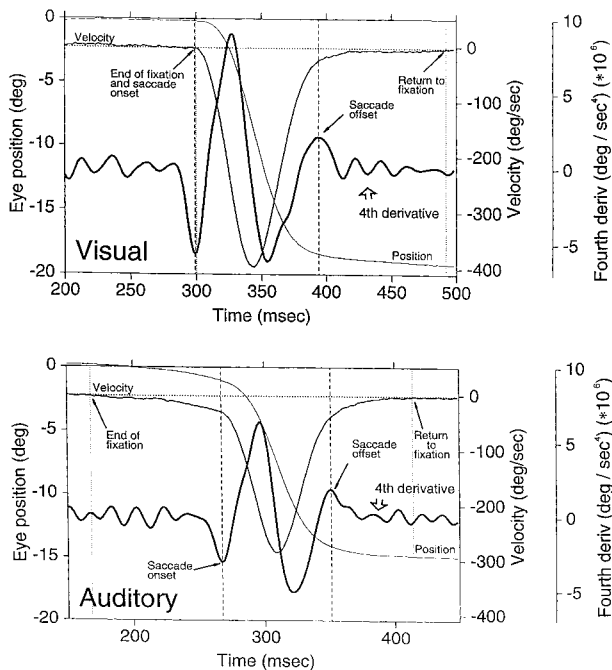


FIG. 2. End of fixation and saccade onset and offset criteria. Horizontal component of eye position (thin trace), its 4th derivative (heaviest trace), and its velocity (intermediate trace), are plotted as a function of time. Horizontal dotted line indicates the 2 SD criterion we used to determine the end of fixation, and the vertical thin dotted lines mark both the end of and return to fixation times. Saccade onset and offset, illustrated by vertical dashed lines, are defined by the 1st and 4th prominent peaks in the 4th derivative trace, respectively.

Saccade dynamics

Having established the presence of a slow eye movement before saccades to noise stimuli in the standard-saccade task, we tested whether the saccadic components of the responses to visual and acoustic stimuli are different. Figure 4 illustrates the same velocity data plotted in Fig. 1, but synchronized to saccade onset, which effectively removes the slow velocity ramp. The traces corresponding to the visual trials remain essentially unchanged (cf. Figs. 1C and 4A), but those from acoustic trials are now better aligned in time showing a more typical saccadic profile (cf. Figs. 1D and 4B). Thus the velocity profiles of eye movements to visual and acoustic targets, when synchronized to saccade onset, are now very similar. The maximal velocity of the saccades to the acoustic target is smaller due to the smaller amplitude of the undershooting movements to acoustic targets.

To assess quantitatively whether the saccadic component of

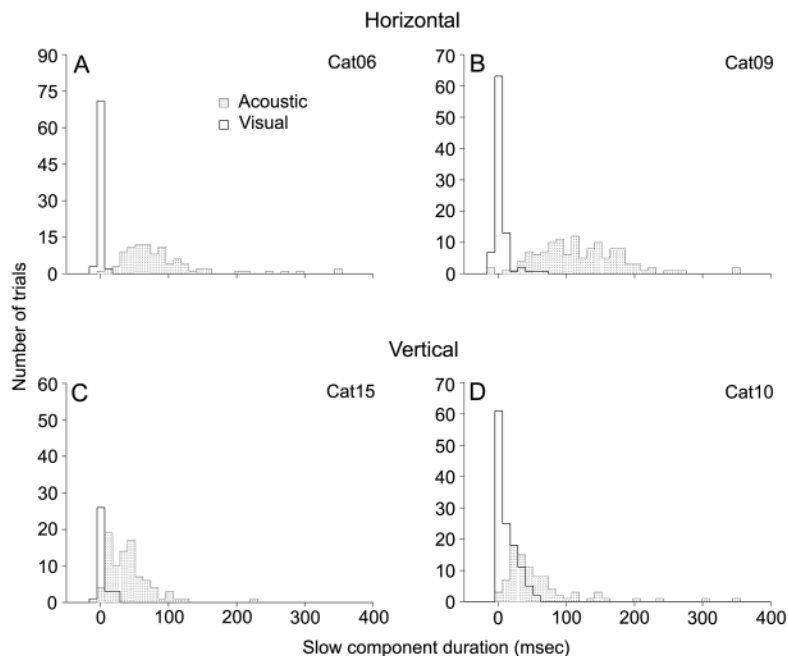


FIG. 3. Distributions of duration of slow component for horizontal (*A* and *B*) and vertical (*C* and *D*) targets. These data represent the time elapsed between the end of fixation and saccade onset as measured in eye movements to 4 horizontal ($\pm 18^\circ, 0^\circ$; $\pm 9^\circ, 0^\circ$) and 4 vertical ($18^\circ, 0^\circ$; $9^\circ, 0^\circ$; $-14^\circ, 0^\circ$; and $-23^\circ, 0^\circ$) targets. Data are collapsed for visual (\square) and acoustic (\blacksquare) targets.

eye movements to long-duration acoustic targets is similar to saccades to visual targets, we compared the slopes of the main sequences, i.e., the relationship between peak saccade velocity and amplitude. Because of the symmetry of the data, the main sequences from leftward and rightward saccades (Fig. 5, *A* and *B*), as well as upward and downward (Fig. 5, *C* and *D*), were collapsed and plotted with a positive slope. The results were consistent across all five subjects studied (Table 2): the slopes of the regression lines fitted to the main sequence of saccades to acoustic and visual targets were not significantly different for horizontal or vertical targets ($P > 0.05$; test for significance of the difference between independent β s) (Cohen and Cohen 1975) in any cat.

Although there were no significant differences between the

slopes of main sequences of upward and downward saccades, there was nonetheless a trend for shallower slopes in downward saccades. This trend is consistent with the presence of a prolonged deceleration in downward eye movements, a “dynamic undershoot” as defined by Bahill et al. (1975). This dynamic undershoot is illustrated in Fig. 6, which shows the velocity of leftward eye movements to a target at $(-18^\circ, 0^\circ)$ (\cdots) and downward eye movements to a target at $(0^\circ, -23^\circ)$ ($-$), all plotted synchronized to the point of maximal velocity. Notice that while the eyes stopped moving horizontally within ~ 100 ms after peak velocity, the eyes continued to move vertically > 100 ms after peak velocity. In all subjects, downward eye movements displayed a deceleration tail that was significantly longer than that observed in horizontal eye movements ($P < 0.05$).

TABLE 1. *Slow component duration*

		Horizontal				Vertical			
		Visual		Auditory		Visual		Auditory	
	Subject	Duration, ms	<i>n</i>	Duration, ms	<i>n</i>	Duration, ms	<i>n</i>	Duration, ms	<i>n</i>
Standard saccade long-duration stimuli	<i>Cat 06</i>	-0.5 ± 2.8	76	87.1 ± 64.4	95	7.44 ± 1.2	85	55.4 ± 35.8	75
	<i>Cat 07</i>	0.0 ± 8.7	132	29.3 ± 37.9	85	3.7 ± 15.2	125	46.1 ± 54.3	48
	<i>Cat 09</i>	3.7 ± 10.9	128	120.8 ± 62.4	125	30.2 ± 26.9	105	90.8 ± 65.6	71
	<i>Cat 10</i>	2.3 ± 7.0	106	49.5 ± 50.5	86	12.3 ± 1.2	122	59.5 ± 59.6	89
	<i>Cat 15</i>	0.5 ± 6.9	107	39.4 ± 40.2	68	2.3 ± 7.4	33	42.0 ± 33.6	88
Delayed saccade long-duration stimuli	<i>Cat 06</i>	-0.8 ± 2.8	19	12.4 ± 17.2	35	—	—	—	—
	<i>Cat 15</i>	2.5 ± 11.8	62	21.2 ± 24.4	93	—	—	—	—
Standard saccade transient stimuli	<i>Cat 06</i>	3.9 ± 11.1	77	4.2 ± 11.9	57	—	—	—	—
	<i>Cat 15</i>	8.6 ± 20.9	76	6.7 ± 10.4	56	—	—	—	—

Values are means \pm SD.

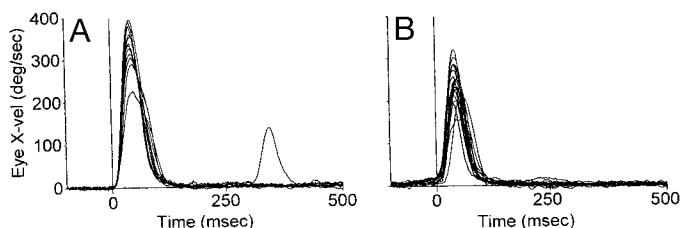


FIG. 4. Eye velocity traces from horizontal eye movements to visual (A) and acoustic (B) targets located at $(18^\circ, 0^\circ)$ plotted synchronized to saccade onset. These data are also shown in Fig. 1 where they are plotted synchronized to the end of fixation. Notice the alignment of the peaks of the velocity traces in acoustic trials.

Effects of time of exposure to the target before behavioral response

In the data presented in the preceding text, the cat was expected to make a saccade to the location of a long-duration visual or acoustic target, the presentation of which coincided with the offset of the fixation LED. To examine the effects of time of exposure to the target on the kinematics of the responses, we used both longer and shorter exposure times. Longer times were achieved using the delayed-saccade task, which forced the cat to listen to the stimulus for the duration of the delay before allowing a response. Shorter times were implemented using the standard-saccade task with transient stimuli, which were much shorter than the saccade reaction time and, therefore, required the cat to respond from memory.

EYE MOVEMENTS IN THE DELAYED-SACCADE TASK. In this condition, the offset of the fixation light, which was the signal for the cat to respond, occurred 300–700 ms after target onset; different delays were used to prevent the cats from anticipating. The velocity profiles of delayed saccades from the 500-ms delay condition from *cat 06* are presented in Fig. 7A with corresponding distributions of the duration of slow component in Fig. 7B. Similar results were obtained from *cat 15*. The longer exposure to the targets affected the kinematics of eye

movements to acoustic but not visual targets. Inspection of these velocity data reveals that eye movements to long duration acoustic targets in the delayed-saccade task are much more similar to eye movements directed to visual targets (Fig. 1C) than those directed to identical broadband noise targets in the standard-saccade task (Fig. 1D). Although the slow velocity ramp was still present (Fig. 7B), its duration was shorter than in the standard-saccade task (Fig. 3A). The slopes of the regression lines fit to the main sequences from delayed saccades to acoustic and visual targets (Table 2) were not significantly different from those obtained from standard saccades for each stimulus condition and each subject separately ($P > 0.05$).

EYE MOVEMENTS TO TRANSIENT STIMULI. We found that shortening the time of exposure to the acoustic target, which requires the cat to respond to the target from memory, essentially abolished the slow velocity ramp. Figure 7C shows the velocity profile of *cat 06*'s eye movements to a single 100- μ s click target located at $(-18^\circ, 0^\circ)$. Clearly, the initial stage of these movements does not show the slow velocity ramp that characterizes eye movements to long-duration broadband noise targets. Instead they are similar to saccadic eye movements to visual targets, as corroborated by the lack of significant differences ($P > 0.5$) between the distributions plotted in Fig. 7D. The slopes of the main sequences computed from standard saccades to acoustic and visual transient stimuli were similar, and they were also similar to those computed from standard saccades to long-duration targets (Table 2). Comparable results were obtained from *cat 15*.

Summary

A summary of the duration of the slow velocity ramp for horizontal eye movements measured in the various experimental conditions from two subjects (*cats 06* and *15*) is shown in Fig. 8. The mean duration of the velocity ramp was negligible for visual targets in the standard- and delayed-saccade tasks. In

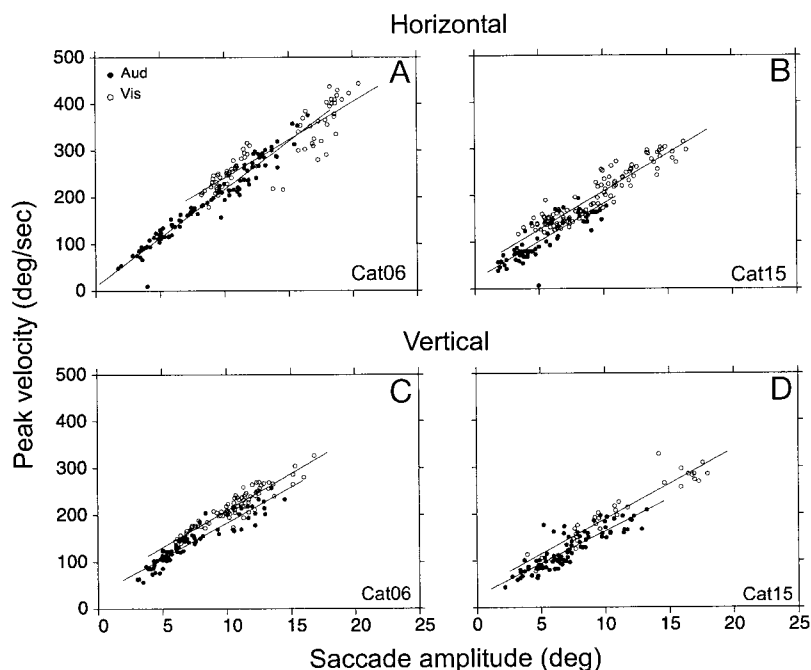


FIG. 5. Representative main sequence plots from standard-saccades to long-duration horizontal (A and B) and vertical (C and D) targets from 2 subjects. Data from leftward and rightward, as well as upward and downward, saccades are collapsed and are presented with positive values. ● and ○ represent data from saccades to acoustic and visual targets, respectively.

TABLE 2. *Main sequence slopes*

	Subjects	Horizontal		Vertical	
		Visual	Auditory	Visual	Auditory
Standard saccade	<i>Cat 06</i>	16.3	20.7	15.8	15.2
long duration	<i>Cat 07</i>	15.6	16.1	18.3	20.1
stimuli	<i>Cat 09</i>	11.3	12.9	14.8	25.0
	<i>Cat 10</i>	14.6	15.2	15.3	16.4
	<i>Cat 15</i>	16.3	16.1	14.9	13.8
Delayed saccade	<i>Cat 06</i>	14.8	16.3	—	—
long-duration	<i>Cat 15</i>	17.7	10.1	—	—
stimuli					
Standard saccade	<i>Cat 06</i>	19.3	18.4	—	—
transient	<i>Cat 15</i>	14.0	10.3	—	—
stimuli					

Values are in degrees per second per degree.

acoustic trials, on the other hand, the duration of the slow velocity ramp changed systematically across the three different conditions studied. For both cats, there was an orderly reduction in the mean duration of the velocity ramp from the long-duration stimuli to the transient stimuli, with intermediate duration recorded in delayed saccades. In both cats, all conditions were significantly different, except that for *cat 06* the duration for transients was shorter than for delay-saccades but did not reach significance.

DISCUSSION

Methodological considerations: saccade onset criterion

Central to the thesis of this paper is the accurate detection of saccadic eye movement onset. In visual trials, this was straight forward because the eye movements of our cats showed the typical abrupt onset that characterizes saccadic eye movements in various species (Becker and Fuchs 1969; Evinger and Fuchs 1978; Fuchs 1967). In acoustic trials, however, saccadic eye movements were preceded by a slow velocity ramp of variable duration (Fig. 1) so that the onset of the saccadic component was delayed. A common criterion used to mark the onset of saccades is to use some minimum velocity threshold, e.g., Waitzman et al. (1991). However, we found this unsatisfactory because the different slopes and durations of the slow velocity ramp led to underestimates of saccade onset in some trials and

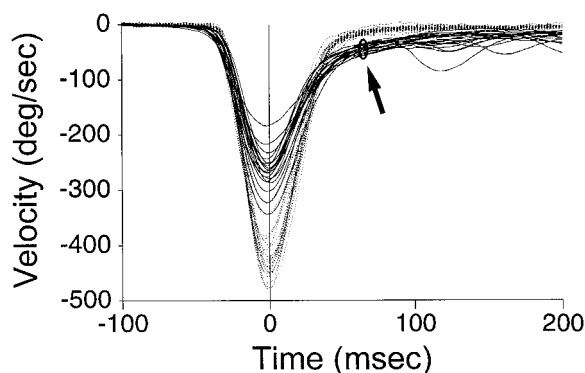


FIG. 6. Dynamic undershoot. Velocity traces from eye movements to visual targets located at $(-18^\circ, 0^\circ)$; $(0^\circ, -23^\circ)$; $(0^\circ, -23^\circ)$; $(0^\circ, -23^\circ)$. All trials are plotted synchronized to the peak velocity. Notice the slower return of the eye to the fixation state for downward saccades (\uparrow).

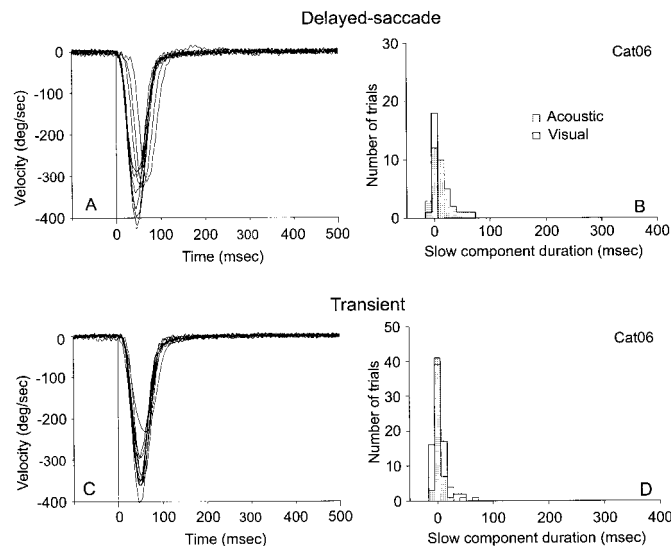


FIG. 7. Eye movement data from the delayed-saccade (A and B) and transient (C and D) conditions. Eye velocity profile from delayed-saccade trials to a long-duration acoustic target (A) at $(-18^\circ, 0^\circ)$ plotted synchronized to the end of fixation. Distributions of the slow velocity ramp duration are shown in B. Notice the shorter duration of the ramp in these auditory trials compared with those in Fig. 3. C: eye velocity profile from standard-saccade trials to a single $100\text{-}\mu\text{s}$ click target at $(-18^\circ, 0^\circ)$ also plotted synchronized to the end of fixation. Notice the absence of the slow velocity ramp in these acoustic trials. Distributions of the slow velocity ramp duration for the acoustic and visual (25-ms duration) transient conditions are shown in D.

overestimates in others and because velocity thresholds that were high enough to accommodate all acoustic trials did not coincide with saccade onset in visual trials as selected by the end-of-fixation criterion. Empirically, we found that the first prominent peak of the fourth derivative of position was a reliable measure of saccade start for it produced results consistent with those of the end of fixation criterion in visual trials (Figs. 3 and 8).

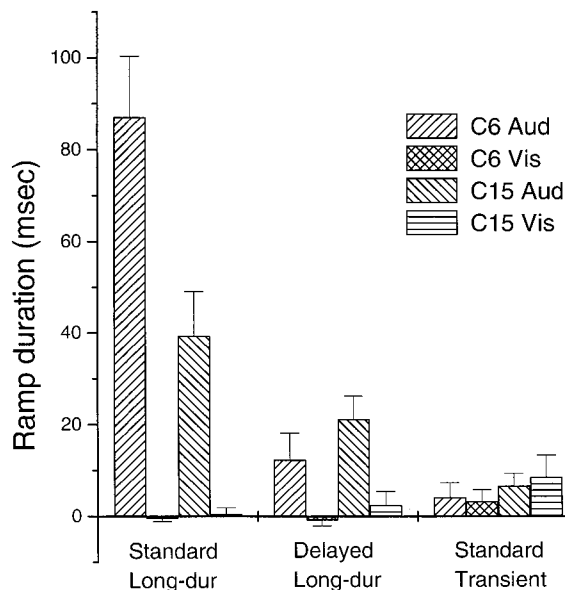


FIG. 8. Summary of the mean duration of the slow velocity ramp from horizontal eye movements to a target at $(18^\circ, 0^\circ)$ for the 3 experimental tasks used. Data are plotted separately for each subject. Standard bars represent confidence intervals ($2 \pm \text{SE}$ of the sample mean).

Slow component

The present results show that saccadic eye movements of cats to long-duration broadband noise targets, unlike those to similar visual targets, are preceded by a slow velocity ramp of variable duration. This eye movement is unlikely to be an artifact of our recording system or the result of damage to the eye during surgery because it was not observed in eye movements to visual targets. To our knowledge, this type of eye movement has not been described in the literature.

In the delayed-saccade task, the cat was compelled to listen to the acoustic stimulus for an additional period before responding. This resulted in slow components of much shorter duration than in the standard-saccade condition (Figs. 3, 7, and 8).

The systematic changes in slow component duration observed across the acoustic conditions lead us to hypothesize that its presence in the standard-saccade condition to long-duration signals is due to uncertainty about the actual position of the target. It appears as if the cats were able to determine the general location but not the actual position of the acoustic target at the time of end of fixation. Thus they began to move their eyes slowly in the general direction of the target while waiting for additional information about its actual location and made a saccade only after the uncertainty was resolved.

The lack of a slow component before saccades to transient acoustic targets (Fig. 7) also appears to support our hypothesis. In the transient stimulus condition the 100- μ s target expired well before the end of fixation, so that there was no additional information to be gained by waiting to make a saccade.

Anticipatory eye movements, qualitatively similar to the slow component we report here, to visual, but not acoustic, targets have been previously reported in human subjects: before smooth pursuit (Becker and Fuchs 1985; Boman and Hotson 1988; Kowler and Steinman 1979a) and saccadic eye movements (Kowler and Steinman 1979b; Moschner et al. 1996) to visual targets moved in a predictable direction. Eye movements of this type have been attributed to the subject's expectations for the target to move. Because the acoustic targets used in our experiments did not provide a retinal signal nor could our subjects predict the position of upcoming targets, the mechanisms underlying these anticipatory eye movements to visual and acoustic targets are likely to be different.

Saccade dynamics

When the target for a saccade is nonvisual, the dynamics of the movement are reported to be different, although there is no unanimity. Slower peak velocities have been observed in human (Engelken and Stevens 1989; Zahn et al. 1978; Zambarbieri et al. 1982) and monkey (Russo and Bruce 1994) saccades to acoustic targets. Whittington et al. (1981), on the other hand, reported no differences in the kinematics of saccadic eye movements to visual and acoustic targets in monkeys trained to localize sound. The limited description of the methods and the lack of representative kinematic data in both Russo and Bruce (1994) and Whittington et al. (1981) make it difficult to evaluate their results.

The similarity of the slopes of the regression lines fitted to the main sequences of saccades to horizontal and vertical acoustic and visual targets in all five subjects suggests that the

saccade burst generator was engaged in a similar manner regardless of the type of target. The different levels of experience of our subjects, which included a novice cat (*cat 09*), suggests that practice did not play a role in shaping the dynamics of the saccades.

The slopes of the regression lines fit to the main sequence of both horizontal and vertical saccades were slightly steeper than those reported by Evinger and Fuchs (1978) for two subjects: 13.5 and 9.0°/s/° for horizontal movements, and 14.1 and 17.6°/s/° for vertical movements. Differences in the experimental procedures could account for the steeper main sequences obtained in the present study. Such differences may be subtle and thus difficult to relate to the data. For instance, Evinger and Fuchs (1978) presented a tone that sounded continuously when the eyes of the cat were within 2° of the target.

Most models of the oculomotor system propose that saccades are executed by the discharge of burst neurons, which carry the desired velocity information of the impending saccade (Fuchs et al. 1985; Robinson 1975). The velocity, or pulse, then is integrated by a neural circuit to derive the position, or step, signal of the saccade. Both the pulse and step then are sent to the oculomotor plant to generate the saccade. The slow eye movement preceding saccades to acoustic targets is novel, and in this model could be generated by a small ramp velocity signal to the burst neurons.

Last, the differences in dynamics observed between downward and upward eye movements are consistent with the results of André-Deshays and Ron (1992) and Collewijn et al. (1988) in humans under both head-fixed and -free conditions. The origin of the differences is unknown, but asymmetries in the head-neck musculoskeletal system have been suggested as the potential source (André-Deshays and Ron 1992).

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