



Research paper

The eccentricity effect for auditory saccadic reaction times is independent of target frequency

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ABSTRACT

Although much is understood about the stimulus properties affecting the latency of saccadic eye movements to visual targets, relatively little is known about the properties affecting saccades to auditory targets. This study examined the effect of three primary acoustic features—frequency, intensity, and spatial location—on auditory saccade characteristics in humans, and compared them to visual saccades. Saccade targets were presented from an azimuthal array of speakers and LEDs spanning $\pm 36^\circ$. There was an ‘eccentricity effect’ for auditory saccades such that latencies decreased by up to 70 ms with eccentricity. This was observed for all frequencies and intensities tested. There was a smaller effect in the opposite direction effect for visual saccades. Auditory saccades had similar latencies to visual saccades (within 5 ms) for near midline locations, but were up to 90 ms faster at eccentric locations ($\pm 36^\circ$). Overall, saccadic latencies were shortest for wideband noise and narrowband noises with center frequencies falling within the human speech range. Examination of saccade accuracy showed decreasing accuracy with increasing eccentricity, and a negative correlation between accuracy and latency for auditory stimuli.

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1. Introduction

While humans rely primarily on the visual system for navigating the world, the auditory system also provides substantial input to orienting processes (see Middlebrooks and Green, 1991; Sparks and Nelson, 1987, for review). Acoustic events can provide useful information regarding the location of a stimulus, particularly in conditions of visual crowding or when the event is outside the visual range. To use auditory information effectively the sound source must be localized, a process that relies on the encoding of location-dependent variations in the timing and intensity of a sound arriving at the two ears (Middlebrooks and Green, 1991; Yost and Sheft, 1993). The interaural time difference (ITD) is primarily coded through low-frequency neural channels (<1500 Hz; Middlebrooks and Green, 1991). Higher frequency sounds (>1500 Hz), but not low-frequency sounds, are subject to diffrac-

tion by the head and pinna of the receiver, resulting in an energy reduction of the sound wave prior to arrival at the far ear and producing intensity cues both binaurally (interaural level differences, ILDs) and monaurally (spectral filtering differences) (Middlebrooks and Green, 1991; Shaw, 1974; Shaw and Vaillancourt, 1985). For both binaural cues (ITDs and ILDs) maximal disparities are observed for peripheral sound sources of 90° (Mills, 1958).

Saccadic eye movements are generated by the oculomotor system in order to bring a peripheral target of interest into the region of high-acuity fovea. Sensitivity to auditory signals has been demonstrated in neural regions involved in saccade production such as the primate superior colliculus (SC) (Cynader and Berman, 1972; Drager and Hubel, 1975, 1976; Gordon, 1973; Meredith and Stein, 1986; Pollack and Hickey, 1979; Sparks, 1986) and the frontal eye fields (FEF), (Bruce and Goldberg, 1985a,b; Russo and Bruce, 1994; Schall, 1991). Further, both humans (Frens and van Opstal, 1995; Mondor and Zatorre, 1995; Spence and Driver, 1994; Zahn et al., 1978, 1979; Zambbarbieri et al., 1982) and monkeys (Populin, 2006) are capable of generating saccadic eye movements in response to targets exclusively in the auditory modality.

There is an ‘eccentricity effect’ for auditory saccades; saccadic reaction time (SRT) decreases as a function of increasing target eccentricity (Frens and van Opstal, 1995; Goldring et al., 1996; Lueck et al., 1990; Yao and Peck, 1997; Zahn et al., 1979; Zambar-

Abbreviations: SRT, saccadic reaction time; ITD, interaural time difference; ILD, interaural level difference; SC, superior colliculus; FEF, frontal eye fields; RF, receptive field; LED, light-emitting diode; EOG, electrooculography; FP, fixation point; CF, center frequency; SPL, sound pressure level; dB, decibel.

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bieri et al., 1982). The opposite relationship between SRT and target eccentricity has been demonstrated for the visual modality (Cohen and Ross, 1977; Goldring et al., 1996; Kalesnykas and Hallett, 1994; White et al., 1962; Yao and Peck, 1997; Zambarbieri, 2002). The mechanism underlying the eccentricity effect for auditory SRT is not currently known, but it has been proposed that auditory saccadic latency may be related to spatial receptive field characteristics of neurons in the SC or FEF (Zambarbieri et al., 1982, 1995; Zambarbieri, 2002) for at least two reasons: (1) the eccentricity effect shifts with eye position (Yao and Peck, 1997; Zambarbieri, 2002), as do the spatial receptive fields of many neurons in the SC (Jay and Sparks, 1984) and FEF (Schall, 2004); and (2) the “gap effect”, whereby SRT is reduced when the fixation point is removed prior to the onset of the target, is present for both visual (Munoz et al., 2000) and auditory saccades (Zambarbieri, 2002). The gap effect is known to be related to SC processing (see Munoz et al., 2000 for a review). If the eccentricity effect is related to the spatial receptive fields in the SC, as has been proposed (Zambarbieri et al., 1995), then it may not be observed for low-frequency sounds, as they appear to contribute little to auditory spatial receptive field structure in the SC (Campbell et al., 2006), which is dominated by higher frequency monaural and binaural intensity cues and not modulated by variations in low-frequency ITDs (Campbell et al., 2006). To date, the eccentricity effect for auditory saccades has only been examined with wideband noises of a single intensity (Corneil and Munoz, 1996; Corneil et al., 2002; Frens and van Opstal, 1995; Zambarbieri et al., 1995; Zambarbieri, 2002), which contain all cues to sound location. Frens and van Opstal (1995) examined saccadic latency to tones at different eccentricities; however, they did not show the results separately and pure tones are poorly localized, especially in elevation as they provide no substrate for monaural spectral cues. Thus, a comparison of the eccentricity effect has not been reported across stimuli that selectively engage the low-frequency interaural time difference processing mechanisms and those which selectively engage the higher frequency interaural level difference and monaural spectral processing cues. We examined this in Experiment 1 by using narrowband noises of different center frequencies as stimuli. In Experiment 2, we examine the effect of stimulus intensity on the eccentricity effect using wideband stimuli.

2. Materials and methods

2.1. Subjects

All paradigms were reviewed and approved by the Queen’s University Human Research Ethics Board. Seventeen healthy subjects (nine males, eight females), ranging from 24 to 55 years of age, participated in the experiments. Most subjects had previously participated in eye movement experiments using visual but not auditory targets. All subjects were informed of the general nature of the study and consented to participate before the experiments commenced. Subjects requiring corrective lenses for mild myopic vision were able to keep them intact for the duration of the experiment. Subjects had no known ocular, acoustic, or pathological neural symptoms.

2.2. Experimental design

Subjects were seated on a customized chair (0.6 m + 0.05 m cushion in height) in the center of a light-tight, sound-attenuated room in which all major surfaces were lined with 3” acoustic foam (Auralex). A nine-speaker array, each equipped with a small light-emitting diode (LED, 1 cd/m²), was positioned along a horizontal platform at eye level (1.35 m from floor), and hidden behind a

sheer black fabric, which reduced LED luminance to 0.05 cd/m² (Minolta CS100 light meter). The speakers (AuraSound, 2 in. diameter extended range loudspeaker, model NSW2-326-8A) were circular and had a flat frequency response for the sound frequencies used in this study. The nine speakers in the array were chosen out of a large pool of speakers based on sound spectrum similarities, as measured by a sound pressure meter (Bruel & Kjaer model #2239A, A-weighted). The center speaker was not programmed to play a sound and acted solely as the LED fixation point (FP) to center the subject’s gaze axis before each trial. To prevent head movements, subjects were instructed to place their chin in a chinrest and to locate targets with their eyes only. The apparatus was adjusted according to the height of each individual subject to ensure that each subjects’ head was centered in the room.

Horizontal eye movements were recorded with direct current electrooculography (EOG) (von Noorden and Burian, 1958). Two Ag–AgCl skin electrodes were placed temporally (i.e., between each eye and the temple) and a third reference electrode was placed on the forehead, between the eyebrows. The signal was amplified by 2000 and low-pass band filtered below 30 Hz with a direct current preamplifier (Grass, Model #CP122). Subjects wore the electrodes for approximately 5–10 min before the experiment was initiated to stabilize the signal and minimize EOG drift. To achieve a baseline eye position (i.e., compensate for drift in the EOG signal), subjects were instructed to maintain gaze on the FP while the preamplifier was set to zero. This was repeated after breaks if required.

Sounds were generated digitally with a sampling frequency of 44.1 kHz via MATLAB software running on an Apple Macintosh. Digital sounds were processed through Digital-Analog converter (MOTU 24 I/O), then sent through custom-designed amplifiers (one for each channel) and finally presented through one of eight circular speakers. Timing of sound onset was sensed by a trigger on the output of the amplifier that sent a TTL pulse to REX software (version 7, Hays et al., 1982) on a PC running a real-time UNIX operating system. A custom-designed paradigm running in REX controlled the presentation of trials and co-ordinated the timing of stimulus presentation with 1 ms accuracy (1000 Hz). REX sent an 8-bit value indicating the type of sound required via the UDP protocol (ethernet) to the Macintosh, which was received by MATLAB 5.0 (Mathworks Inc.). REX then waited for a TTL pulse from the sound trigger to confirm sound onset prior to proceeding with the trial. This maintained millisecond timing for the time-sensitive segments of each trial. REX also set the voltage on the LEDs in order to control the presentation of visual stimuli. Timestamps of all stimulus events were sent to Plexon data acquisition hardware (Plexon), which incorporated them with data about the ongoing eye position signal from the EOG (also sampled at 1000 Hz).

Each trial began with the appearance of a central fixation point (FP) lasting 1500 ms. Subsequent to extinguishing of the FP, an eccentric target was presented for 500 ms. The target randomly appeared at an eccentricity of 9°, 18°, 27°, or 36° to the right or left of the FP. Subjects were instructed to look from the FP to the target as quickly and accurately as possible. At the end of the trial, the target was turned off and following a 1000 ms inter-trial interval the FP was illuminated again to initiate the next trial.

2.2.1. Experiment one: sound frequency

Eleven subjects (six males, five females) participated in the experiment, which followed the experimental methods described above. The target was either a LED flash or one of six types of noise bursts. One sound was a wideband noise burst generated digitally with a passband between 0.1 and 1.2 kHz. The other five noises were narrowband and computed with a distinct center frequency (CF) (0.25, 0.7, 1.5, 5.0, and 9.0 kHz) and an equivalent rectangular bandwidth of 2.0. The passband was calculated based on the following equation:

ERB-rate E (in ERB units) = $11.17 \ln[(f + 312)/(f + 14,675)] + 43.0$

where f = frequency in kHz (Moore and Glasberg, 1983). The noises were newly generated for each trial in MATLAB and played at sound pressure levels (SPLs) customized to each speaker, such that a constant decibel (dB) level of 70, measured from the center of the room, was maintained.

There were 56 trial-types (8 locations \times 7 stimulus types) and a total of 20 repetitions were obtained for each. These data were acquired in two sessions (usually on different days). In each session trials were presented in two or three blocks containing four or five repetitions of each trial type in random orders. Blocks were separated by short breaks in order to help maintain alertness. The first session was preceded by a practice session that included two repetitions of each trial type in random order. Practice data were not analyzed.

2.2.2. Experiment two: sound intensity

Six subjects (three male, three female) participated in this experiment, which followed the same experimental set-up described above. The target was a wideband noise burst (pass-band = 0.1–1.2 kHz) newly generated for each trial with one of three intensity levels—55, 65, or 75 dB. The subjects performed one session consisting of 20 repetitions of each of 24 trial-types (8 locations \times 3 stimulus intensities) and presented in four blocks of five repetitions. Blocks were separated with breaks to help maintain alertness. The first session was preceded by a practice session comprising two repetitions of each trial type in random order. Practice data was not analyzed.

2.3. Data processing and analysis

Data were analyzed on a PC using a custom-designed automated saccade detection program running in MATLAB, which marked the onset and endpoint of the primary saccade. The marks were then displayed visually on the velocity trace of the saccade in order to be verified and manually corrected if necessary. Trials in which subjects showed an anticipatory reaction (SRT < 90 ms), an inattentive reaction (SRT > 600 ms), or failed to make a saccade at all, were eliminated from further analysis.

To ensure subjects were localizing the targets, we also measured the accuracy of auditory saccades. In order to determine the magnitude of the EOG signal for each saccade, the EOG signal was calibrated at the beginning of the experiment by having subjects shift eye position to the location of known visual targets. Within the range of eccentricities tested here (9–36°), the EOG signal remained linear with eccentricity. The magnitude of the horizontal EOG signal at the endpoints of *visual* saccades were plotted as a function of stimulus location, and for each subject a near perfect linear fit (r 's > 0.9) was obtained. We assumed that the average EOG magnitude at saccade endpoint for each LED location represented the accurate stimulus location, since visual saccades are far more accurate than auditory saccades. We then used the EOG signal magnitude at a given location from the linear fit to compare with each subject's EOG endpoint magnitudes obtained for auditory targets. Evaluations of accuracy were restricted to experiment one because of the presence of the visual target. There is a major limitation of this method, of course, which is that we have only horizontal measures of eye position, and it is possible that subjects were mislocalizing in the vertical dimension. However, in this study we were not so interested in sound localization per se, as we were in the latency of auditory saccades for which the EOG method has excellent temporal resolution.

3. Results

3.1. SRT as a function of frequency and eccentricity

Experiment 1 examined the effects of both frequency and eccentricity on the latency of auditory saccades. The data from Experiment 1 were subjected to a 3-factor (frequency—7, side—2, and eccentricity—4) repeated-measures ANOVA using the Greenhouse–Geisser correction for violations in sphericity (Greenhouse and Geisser, 1959). There was a main effect of frequency [$F(5, 50) = 6.26, p = 0.002$], illustrated in Fig. 1B. Analysis of simple effects showed that subjects had significantly longer SRTs in response to sounds of 0.25 kHz [$F(1, 50) = 12.22, p < 0.01$] and 9.0 kHz [$F(1, 50) = 18.58, p < 0.01$], compared to those of 0.7 kHz, 1.5 kHz, 5.0 kHz, and wideband noise burst. There was also a main effect of eccentricity [$F(3, 30) = 130.082, p < 0.001$], such that SRT decreased with increasing eccentricity. A trend analysis of the relationship between SRT and eccentricity was completed within the repeated-measures ANOVA to determine if the function was best fit entirely by a first-order polynomial (linear trend) or included components from higher order polynomials (quadratic, cubic, etc.). Results showed that this function was mostly accounted for by a linear trend [$F(1, 30) = 331.2, p < 0.01$], with the remaining sums of squares accounted for by a quadratic [$F(1, 30) = 57.3, p < 0.01$]. This is illustrated in Fig. 1C, in which SRTs for each stimulus frequency condition and the visual condition are plotted against stimulus eccentricity. This eccentricity effect was similar for all target frequencies (see Fig. 1C), but there was an interaction between frequency and eccentricity [$F(15, 150) = 2.81, p < 0.05$], which could be accounted for by the 0.7 kHz sound showing a more exponential function with eccentricity compared with the 1.5 and 5.0 kHz sounds which were more linear. There was no main effect of side [$F(1, 10) < 1, ns$], nor an interaction involving the side variable (all p 's > 0.17).

A separate 2-factor repeated-measures ANOVA (modality versus eccentricity) was conducted to compare the eccentricity effect for auditory (wideband noise only) and visual stimuli. There was a main effect of modality [auditory faster than visual, $F(1, 10) = 21.3, p < 0.001$], but not eccentricity [$F(3, 30) = 1.237, ns$]. This was because of a significant modality versus eccentricity interaction in which the eccentricity effect was in opposite directions for the two modalities [$F(3, 30) = 144.17, p < 0.001$], see Fig. 1C.

3.2. SRT as a function of intensity and eccentricity

Experiment 2 examined the effects of both intensity and eccentricity on the latency of auditory saccades. The results from Experiment 2 were subjected to a 3-factor repeated-measures ANOVA (level \times side \times eccentricity). The data are plotted in Fig. 1D. There was a main effect of eccentricity [$F(3, 15) = 90.30, p < 0.001$], but no effect of stimulus intensity [$F(2, 10) = 2.18, ns$] or side [$F(1, 5) < 1$] for the narrow range of intensities used (55–75 dB). There was an interaction between intensity and eccentricity [$F(6, 30) = 3.34, p < 0.05$], which could largely be accounted for by the 55 dB sound showing a more linear function with eccentricity compared to the more exponential function of the 65 and 75 dB sounds. There were no other interactions (all p 's > 0.1).

3.3. Accuracy of saccades to auditory targets (Experiment 1)

In Fig. 2A, population mean saccadic endpoints are plotted against location (relative to the localization of the visual stimuli) separately for each stimulus frequency. All subjects were able to localize auditory targets, as indicated by a strong main effect of eccentricity [$F(3, 30) = 236.8, p < 0.01$]. There was a general ten-

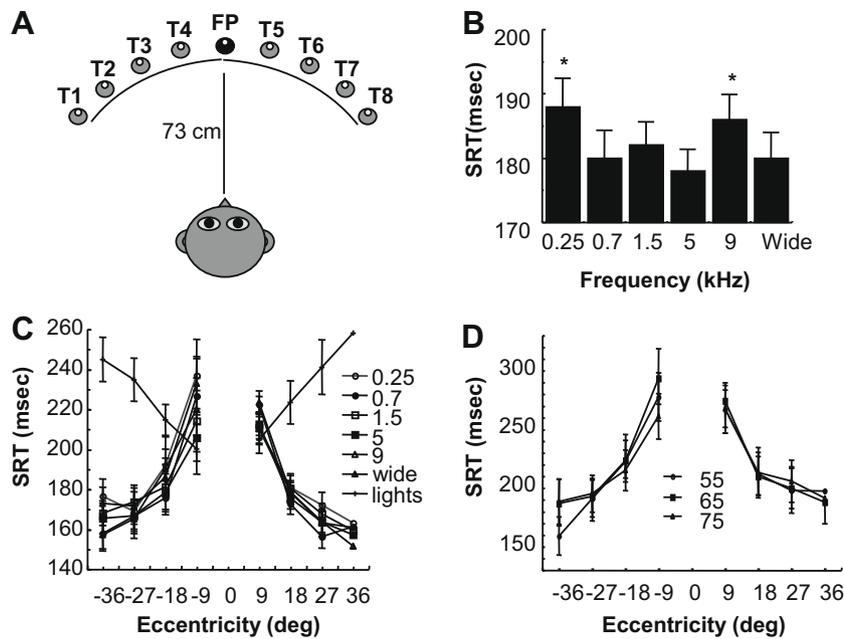


Fig. 1. (A) Schematic of the experimental set-up. Subject is centered in the anechoic chamber facing an azimuthal array consisting of a fixation point (FP; 0°) and eight equally spaced targets (T; ±36, 27, 18, and 9°) hidden from view. (B) Mean saccade latency (±SE) versus stimulus frequency. Data were computed from 15 to 20 individual trials for each of 11 subjects and collapsed across side and location. Asterisks (*) denote statistical significance ($P < .05$). (C) Mean saccade latency (±SE) versus target eccentricity for all subjects in response to seven narrowband noises (2 ERBs wide) with varying center frequencies: auditory—0.25 kHz (open circles), 0.7 kHz (closed circles), 1.5 kHz (open squares), 5.0 kHz (closed squares), 9.0 kHz (open triangles), wideband (closed triangles); visual (plus). Each data point was computed from 15 to 20 individual trials for each of 11 subjects. (D) Mean saccade latency (±SE) versus target eccentricity for all subjects. Targets were wideband noises of three intensities: 55 dB (closed circles), 65 dB (closed squares), 75 dB (closed triangles). Each data point was computed from 15 to 20 individual trials for each of six subjects (Experiment 2).

dency to slightly overshoot the 9° target and undershoot the 36° target. This undershoot was particularly strong for the 0.25 kHz target, and least apparent for the 0.7 kHz target, i.e., there was a main effect of frequency [$F(5, 50) = 6.23, p < 0.001$] and an interaction between frequency and eccentricity [$F(15, 150) = 18.56, p < 0.001$]. There was also an interaction between side and eccentricity [$F(3, 30) = 11.86, p < 0.01$], with the overshooting of the 9° target and undershooting of the 36° target being more pronounced on the left side (not shown).

To determine the variability in sound localization, the mean absolute value of the deviation of saccade endpoint from the localized visual target (absolute deviation) was analyzed as a function of frequency, side, and eccentricity. There was no main effect of frequency [$F(5, 50) = 1.805, ns$] nor any interaction between frequency and eccentricity [$F(15, 150) = 2.67, ns$]. The highest absolute deviation occurred for 1.5 kHz, consistent with a wealth of data showing poorest localization acuity near this frequency because neither binaural cue is coded optimally (Macpherson and Middlebrooks, 2002; Middlebrooks and Green, 1991; Stevens and Newman, 1936). The population average absolute deviation as a function of eccentricity is displayed in Fig. 2B. Absolute deviation increased with eccentricity [$F(3, 30) = 6.63, p < 0.05$]. There was also a main effect of side [$F(1, 10) = 5.42, p = 0.04$], reflecting the greater tendency to undershoot eccentric targets on the left (see localization data above). Since, as with SRT, sound localization accuracy was affected by eccentricity, we looked at the relationship between SRT and accuracy and found a negative correlation ($r = 0.64$; Fig. 2C). Thus, eccentricity has opposite effects on SRT and accuracy.

4. Discussion

We set out to examine the effect of stimulus frequency, intensity, and eccentricity on the latency of auditory saccades. There were two main findings of this study: (1) we replicated the eccentricity effect (decreasing SRT with increasing eccentricity) and

showed that it did not vary much with sound frequency or intensity; and (2) on average, saccades to midrange frequencies were initiated more quickly than those to very low and very high sound frequencies.

4.1. The eccentricity effect for SRTs is not modulated by sound frequency or intensity

We reproduced the eccentricity effect, with SRT decreasing as much as 70 ms between target eccentricities of 9° and 36°. Overall, the saccade latencies observed in this study (~150–240 ms for Experiment 1 and ~150–280 ms for Experiment 2) were slightly shorter than values obtained by others under comparable target array conditions: ~160–340 ms for a 5–40° azimuthal array (Frens and van Opstal, 1995); ~260–350 ms for a 10–80° azimuthal array (Populin, 2008; monkeys); ~290–360 ms for a 10–30° azimuthal array (Yao and Peck, 1997). Our relatively low SRTs are probably accounted for by the fact that our targets appeared with temporal predictability, and that our subjects were generally experienced in eye movement tasks. It is interesting to note, however, that a robust eccentricity effect is observed even under conditions of temporal predictability.

This study revealed that the relationship between SRT and eccentricity was not modulated by variations in frequency or intensity of sound, suggesting that the auditory signals reaching the neural machinery initiating eye movements are independent of these key acoustic properties and are supported equally by both interaural time and interaural intensity cues to sound location.

We also found a strong effect of eccentricity on visual SRT in the opposite direction to that of auditory SRT (Fig. 1C). Subjects were faster to orient to LEDs located close to the midline by up to 50 ms compared to the most eccentric location. Previous experiments have found smaller variations in SRT for visual stimuli across the horizontal plane (Cohen and Ross, 1977; Goldring et al., 1996; White et al., 1962; Yao and Peck, 1997; Zambardi,

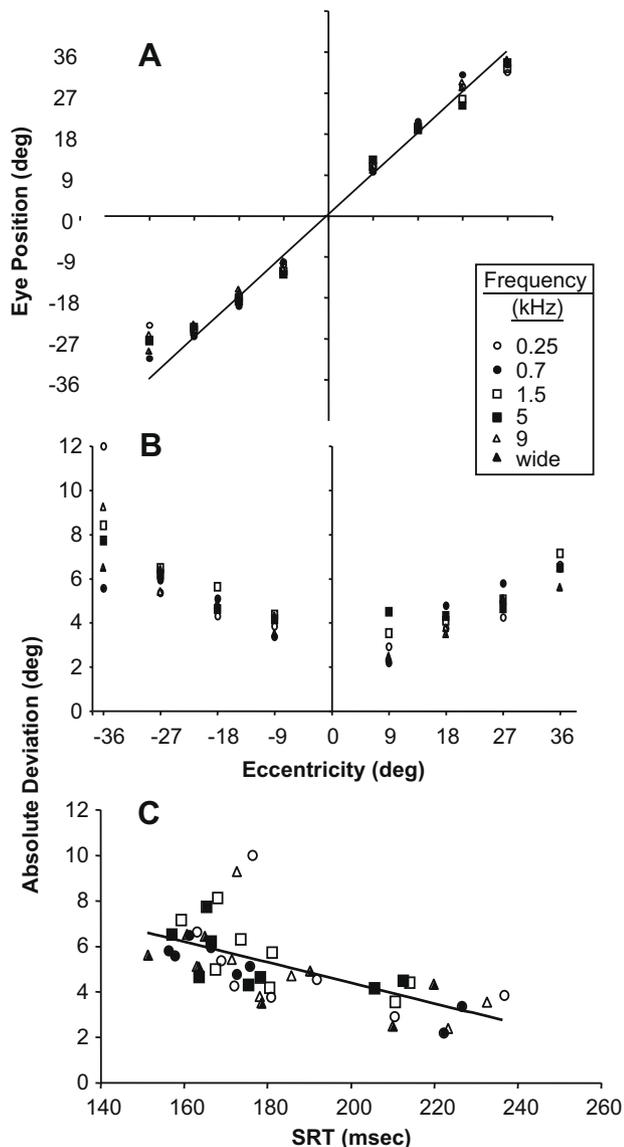


Fig. 2. (A) Eye position versus target eccentricity for eleven subjects in response to six sound stimuli—0.25 kHz (open circles), 0.7 kHz (closed circles), 1.5 kHz (open squares), 5.0 kHz (closed squares), 9.0 kHz (open triangles), wideband (closed triangles)—and a visual stimulus (LED; solid line). Eye position for the two sensory conditions is compared for subject accuracy. Subjects accurately localized hidden auditory targets, with minor overshoots at 9°, and undershoots at 36°. (B) Absolute deviation versus target eccentricity for all subjects in response to six sound stimuli. Data points were computed from 15 to 20 trials for each of eleven subjects. Accuracy of auditory saccades was inferred from the linear fit of the visual saccade endpoints with location. Subjects were worse to localize more eccentric auditory targets. (C) Saccadic latency versus absolute deviation for all subjects in response to six sound stimuli. Data points were computed from 15 to 20 trials for each of eleven subjects. A speed-accuracy trade-off is evident from regression analysis.

2002). Prior evidence also indicates that visual saccades are faster than auditory saccades for eccentricities up to 15° or 20° (Goldring et al., 1996; Yao and Peck, 1997; Zambbarbieri et al., 1982, 1995; Zambbarbieri, 2002); however, results here show that only visual saccades to the 9° target positions were elicited faster than auditory saccades. The finding that visual saccades are faster than auditory saccades only for midline targets was also reported by Jay and Sparks (1990).

Post hoc examinations to investigate these discrepancies in SRT between auditory and visual stimuli indicated that visual SRT was not impacted by the shape of the stimulus array (flat versus azi-

muthal), nor was it the result of having interleaved visual and auditory targets (removal of the auditory conditions had little effect on visual saccadic latency). However, removing the sheer black fabric used to hide the speakers (thereby increasing LED brightness) resulted in a dramatic decrease in visual SRT, by up to 50 ms for eccentric targets ($\pm 36^\circ$) and 30 ms for near midline targets ($\pm 9^\circ$), thus reducing the magnitude of the eccentricity effect. This finding is consistent with recent evidence showing a strong inverse relationship between intensity and SRTs for visual targets (Bell et al., 2006; Li and Basso, 2008; Marino and Munoz, 2009), and with the results of Cohen and Ross (1977) who showed an eccentricity effect for dim visual stimuli but not bright visual stimuli. SRTs in Cohen and Ross were shorter (~ 210 ms versus 240 ms) for bright stimuli, so the lack of eccentricity effect may be due to a floor effect on SRTs. Interestingly, in our present findings with auditory saccades SRT was found to be little affected by intensity (Experiment 2), at least within the 20 dB range we tested. Future studies are required to systematically compare saccades to visual and auditory stimuli varying widely in intensity in order to determine the visual intensity that matches a given auditory intensity in terms of SRT. Such data would go a long way to understanding varying results obtained from using different methodologies, thus explaining the inconsistencies between studies in describing the eccentricity effect.

4.2. Sound localization accuracy

Because our accuracy measurement was limited to the horizontal plane and depended on the presumed accuracy of the visual saccades, we must be cautious in interpreting accuracy measures since any deviations that may have occurred in the vertical dimension were not measured. That being said, we replicated the basic pattern of results seen by others for sound localization accuracy. The absolute deviation from the visual target was about 4° for the midline-most target (9°) and 8–9° for the most eccentric target (36°). These results are consistent with the findings of Jay and Sparks (1990), Makous and Middlebrooks (1990) and Yao and Peck (1997). Makous and Middlebrooks (1990) demonstrated sound localization errors to be as small as 2° for near midline targets and as large as 8° for eccentric targets. Others have reported even larger error spreads across azimuth (Jay and Sparks, 1990; Oldfield and Parker, 1984; Wightman and Kistler, 1992), albeit using other methods of localization. Moreover, we found that the largest deviation in target localization was at 1.5 kHz (data not shown), which is in line with reports from Stevens and Newman (1936). Frens and van Opstal (1995) measured the accuracy of auditory saccades in two dimensions and found that, while the spectral content of the acoustic stimulus affected orienting in the vertical plane, the accuracy of auditory saccades in the horizontal remained relatively constant across tonal and wideband stimuli, consistent with our findings here with narrowband noises of varying center frequencies.

Interestingly, we found a negative correlation between sound localization accuracy and auditory SRT. Although subjects were faster to initiate a saccade to eccentric targets, they were less accurate at localizing them. It seems, therefore, that there exists a speed-accuracy trade-off in the auditory modality, which may be a partial contributor to the observed eccentricity effect. In response to the eccentricity effect on saccade latency, Yao and Peck (1997) suggest that auditory saccades generated toward eccentric targets may be initiated before sufficient location information has been processed centrally. While the authors dismiss location ‘guessing’ as an explanation for their findings, this explanation is consistent with our observation that rapid auditory SRT appears to be at the cost of localization accuracy.

Head restraint may also influence accuracy of saccades to auditory targets. Populin (2006) showed that monkeys were able to localize sounds more accurately and with less variability when they could move their heads freely, compared to when their heads were restrained by the experimental apparatus (see also Tollin et al., 2005 for a similar result in cats). Likewise for humans, Perrett and Noble (1997a,b) and Wightman and Kistler (1999) have performed sets of experiments supporting the hypothesis first investigated by Wallach (1940) that suggests head movements facilitate sound localization by reducing ambiguities in interaural differences at some locations. In all cases natural head movements enhance a listener's localization accuracy in both the horizontal and vertical planes, even in subjects that make large localization errors when the head is restrained. Moreover, Vliegen and colleagues (2004) observed goal-directed head and eye movements toward a sound source, and reported that intervening head movements did not impede localization accuracy. Because subjects in our study were directed to locate the auditory targets only with their eyes only, head restraint may have acted as an intruding variable in overall accuracy performance.

4.3. Saccadic latency is reduced for midrange frequencies

Unexpectedly, we found that saccades were initiated more quickly toward auditory stimuli of midrange frequencies (0.7, 1.5, and 5.0 kHz, and wideband), when compared with both the lowest (0.25 kHz) and highest (9.0 kHz) frequency, and that this effect was independent of stimulus location. In line with evidence showing that processing speed in auditory centers is influenced by sound frequency (Woods and Alain, 1993), and that the firing rates of individual neurons in primary auditory centers are consistent with the behavioral ability to localize various auditory stimuli (Recanzone, 2000), this frequency preference may be in line with the idea of an acoustic fovea, with highest auditory acuity occurring for frequencies falling within the range of human speech. A similar preference for species-specific frequencies has been found in monkeys (see Wang, 2000), i.e., a greater cortical representation of vocal spectrum frequencies and stronger neuronal discharge rates. Because response speed towards species-specific vocalizations is of critical importance for highly social animals, particularly primates (see Belin, 2006), speeded processing of sounds in the human speech range may be the result of evolutionary pressures to organize and attend to highly valuable acoustic information.

4.4. Conclusion and future directions

The eccentricity effect for auditory saccades is a robust finding which occurs across frequency and intensity. This is a large effect for which the neurophysiological basis is still unknown, and which should be exploited as a way to understand the sensory-motor transformation by which saccades are generated to auditory targets. Further experimental evidence should also be gathered regarding the modulatory effect of target position with respect to the eye, as the latency of saccades to auditory targets is known to be dependent on eye position (Zambarbieri et al., 1995). For visual targets it is known that the magnitude of the visual response in visual-motor neurons of the superior colliculus is negatively correlated with SRT (i.e., the larger the visual response, the shorter the SRT; cat: Gordon, 1973; monkey: Dorris et al., 2002). If the same coding scheme holds for auditory saccades, this would suggest that auditory targets at more eccentric locations elicit larger neural responses. This is actually true of most auditory centers (i.e., the inferior colliculus and auditory cortex), which have neurons with broad spatial receptive fields that typically span the contralateral hemifield with a broad peak in firing at eccentric locations and sharp decreases in firing across the midline (e.g., Stecker et al.,

2005). However, it is not supposed to be true of saccadic generating centers like the superior colliculus in which a more organized map is thought to exist (Cohen and Knudsen, 1999). Future recording studies in the superior colliculus of monkeys actively localizing sounds should provide the answer.

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