



# Saccade Latency Toward Auditory Targets Depends on the Relative Position of the Sound Source with Respect to the Eyes

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**The latency of saccadic eye movements evoked by the presentation of auditory and visual targets was studied while starting eye position was either 0 or 20 deg right, or 20 deg left. The results show that for any starting position the latency of visually elicited saccades increases with target eccentricity with respect to the eyes. For auditory elicited saccades and for any starting position the latency decreases with target eccentricity with respect to the eyes. Therefore auditory latency depends on a retinotopic motor error, as in the case of visual target presentation.**

Saccadic eye movements    Saccade latency    Auditory targets

## INTRODUCTION

The latency of a saccadic eye movement evoked by the appearance of a real target in space reflects the time required to perform a number of different processes: (i) the release of attention from the current fixation point; (ii) the transmission of sensory afferences associated with target appearance; (iii) the localization of the target; (iv) the decision to make the saccadic movement toward the target; (v) the generation of a saccadic command. The coordinate system encoding target localization depends on the kind of target. Whereas a visual stimulus is localized with respect to the eyes (retinotopic coordinates), an acoustic stimulus is localized with respect to the head (craniotopic coordinates).

In primates, saccade related burst neurons in the deeper layer of superior colliculus (SC) play a very important role in saccade execution (Cynader & Berman, 1972; Robinson, 1972; Schiller & Stryker, 1972; Wurtz & Goldberg, 1972; Wurtz & Albano, 1980; Hikosaka & Wurtz, 1985). They are able to encode a motor error signal in retinotopic coordinates and send it to structures involved in execution (Sparks & Mays, 1980). The same cells are active when the motor error signal is generated in response to a non-retinotopic signal as in the case of an auditory stimulus (Jay & Sparks, 1987a). Thus, different stimuli must undergo sensory-motor transformations to access the same motor error map.

Differences in saccade latency may be correlated to this sensory-motor transformation. Provided that the head is still, when visual targets are used to evoke saccadic responses, no difference exists between the reference frame of the sensory information coming from the retina (retinotopic coordinates) and that of the motor error signal. By contrast, a difference in reference frames may occur when saccades are evoked by the presentation of auditory targets which are localized in craniotopic coordinates.

The features of saccadic eye movements evoked by the presentation of visual and auditory targets have already been reported (Zahn, Abel & Dell'Osso, 1978; Zambarbieri, Schmid, Magenes & Prablanc, 1982; Jay & Sparks, 1990).

The present experiments will focus on saccade latency. Our goal is to investigate the process of sensory signal transformation by comparing visual and auditory saccades obtained with an experimental protocol based on three recording sessions differing for the starting position of the eyes in the orbit, before the unpredictable appearance of the target. Evidence that the latency of saccades toward auditory targets depends on the position of the sound source with respect to the eyes provides insights regarding the central processing underlying saccade generation.

## METHODS

Seven subjects (six males and one female, aged between 22 and 25 yr) with normal visual, auditory and oculomotor functions were examined. None of them had previously undergone similar experiments and they were

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naive about the aim of the study. The experiments were performed in total darkness, in a quasi-anechoic room. Subjects were viewing with both eyes and their head was kept in a fixed position by using a bite bar. Subjects were seated at the centre of a circular frame, 220 cm in diameter, supporting visual and auditory targets placed every 5 deg covering an arc of 180 deg in total. Visual targets were red light-emitting diodes (LEDs) with an intensity of 148 cd/m<sup>2</sup>. Auditory targets were 5 cm diameter loudspeakers continuously fed with a 15 Hz square-wave signal so as to produce 60 dB noise bursts.

#### Data recordings

Experiments were controlled by a personal computer equipped with a NATIONAL DIO-24 device for target control and a NATIONAL AT-MIO16 device for signal acquisition. Eye movements were recorded using conventional electrooculography (EOG) by placing two electrodes at both the outer canthi (cyclopean eye recording) and the ground electrode on the forehead. The d.c.-coupled EOG signal was low-pass filtered with cut-off frequency of 40 Hz, sampled at a frequency of 250 Hz and stored for off-line analysis. The estimated resolution of the recording system was about 0.5 deg.

#### Experiments

The EOG signal was calibrated at the beginning of each test. Then a visual target was first presented in order to give the subject a reference point to keep his eyes in a specific position in the orbit. Within each recording session the position of the "visual fixation target" was kept constant at either primary position (condition C0) or 20 deg right or left (conditions C+20 and C-20 respectively) (Fig. 1). Thus each subject underwent six sessions, three for each kind of stimulus (visual or auditory). The trial consisted of a random interval, varying between 2 and 4 sec, during which the fixation target was switched off and a saccade target was presented for 2 sec. In the case of auditory target presentation, the LED, placed in the same lateral position, was then switched on for a further 2 sec.

Saccade targets were located every 5 deg from -35 deg (on the left) to +35 deg (on the right) of the subject's midsagittal plane. In each recording session each target location was activated at least nine times in a random sequence and subjects were asked to fixate the targets as accurately as possible.

Target localization can be expressed using either a craniotopic (target position) or a retinotopic (target displacement) reference system. Target position is the location of the target with respect to the subject's midsagittal plane, target displacement is the position of the target with respect to the eyes.

In condition C0, target position and target displacement were the same since the fixation target corresponded to the primary position of the eyes. In the other two experimental conditions, when the fixation visual target was located at +20 deg, target position differed from

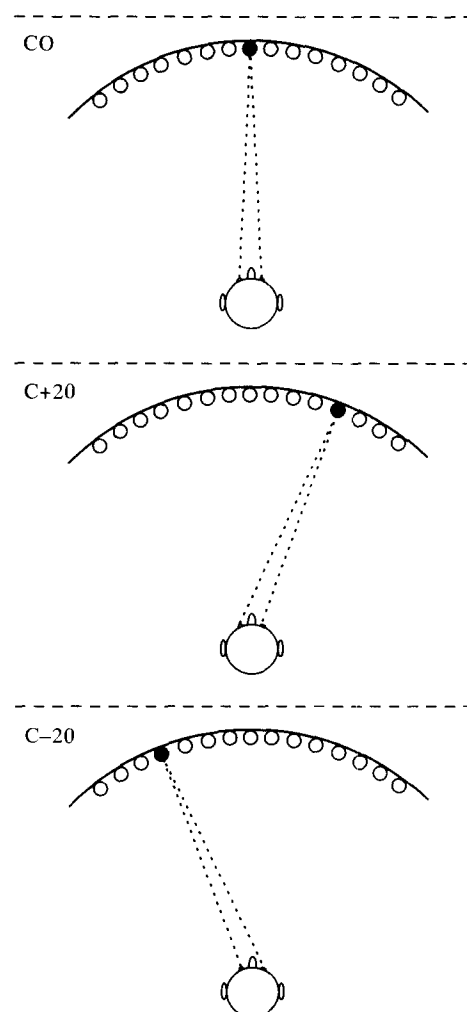


FIGURE 1. Schematic representation of the experimental conditions. The subject is facing a circular frame supporting visual and auditory targets. In the three experimental sessions the visual fixation target was at 0 deg, 20 deg right and 20 deg left respectively defined as condition C0, C+20, and C-20.

target displacement. For the sake of brevity we shall refer to the patterns of eye movement following the presentation of visual and auditory targets as "visual" or "auditory responses" respectively.

#### Data analysis

Quantitative analysis of the saccadic responses was performed by using an interactive program that evaluated the following parameters: latency, duration, amplitude and peak velocity. The beginning and the end of each saccade were determined when eye velocity crossed the 25 deg/sec threshold. Only saccades starting from the fixation target were analysed whereas saccades to the fixation targets were considered as highly predictable and therefore discarded. Moreover, we considered only responses with latencies ranging between 100 and 900 msec, since outside this range responses could have been affected by either anticipatory effects or lack of attention.

We used the SPSS/PC+ program for all statistical analyses and the significant level we chose was  $\alpha = 0.01$ .

RESULTS

Since subjects presented the same trend of data for the same experimental condition, we decided to pool the data from all subjects across conditions. The mean value of latency obtained from the population of subjects in the six experimental conditions are summarized in Table 1, with the corresponding standard deviation and number of observations.

Visual targets

Fig. 2 shows the mean latency vs target position obtained in the three experimental conditions by using visual targets. In condition C0 [Fig. 2(A)] latency increased significantly as target position increased (especially for eccentric target position) regardless of saccade direction. This was confirmed by an analysis of variance (SPSS Manova procedure) with target position as a seven-level factor (we considered the absolute value of target position) and saccade direction as a two-level factor (leftward vs rightward). Results of this analysis were:  $F_{(6,837)} = 12.98$  and  $P < 0.001$  for the target position factor;  $F_{(1,837)} = 3.96$  and  $P = 0.047$  for saccade direction;  $F_{(6,837)} = 0.64$  and  $P = 0.702$  for the interaction between target position and saccade direction. Thus we pooled

latency data from the same target position absolute value. Obviously the same applies to target displacement absolute value.

Now considering the eccentric initial positions, it appears from Fig. 2(B, C) that the C-20 mirrored the C+20 plot with respect to target displacement. To confirm this hypothesis by means of the analysis of variance, we tested the effect of the two-level (C+20 and C-20) fixation target (FT) and the 14-level (from -55 to +15) mirror target displacement (mTD) factors on mean latency values. mTD corresponds to target displacement for condition C+20 and to target displacement changed in sign for condition C-20 (e.g. with mTD the mean latency of C-20 for +55 deg target displacement was compared with the mean latency of -55 deg target displacement of C+20). As we had hypothesized, mTD factor was significant [ $F_{(13,1713)} = 11.29$ ,  $P < 0.001$ ] whereas neither FT [ $F_{(1,1713)} = 0.61$ ,  $P = 0.436$ ] nor the FT\*mTD interaction [ $F_{(13,1713)} = 0.65$ ,  $P = 0.811$ ] were. Thus data from both conditions C+20 and C-20 were pooled into one population (C20) for each target displacement.

The effect of mTD was similar to that previously described for C0 (large mTD show the longer latencies). In addition, for C20 a centrifugal-centripetal asymmetry

TABLE 1. Mean latency values evaluated for each target position and for each experimental condition (C0, C+20 and C-20)

Target position	C0			C+20			C-20		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
<i>Visual</i>									
-35	270.56	52.02	63	264.69	61.48	64	250.32	27.40	62
-30	258.10	33.83	59	258.86	35.48	63	242.10	25.65	59
-25	259.06	35.86	64	257.03	48.15	66	240.73	35.58	60
-20	241.87	29.50	60	248.56	40.83	64	—	—	—
-15	249.51	35.64	61	243.14	39.76	65	218.45	42.45	62
-10	238.53	33.12	60	236.32	39.31	63	224.96	40.82	67
-5	243.52	38.96	59	235.87	32.75	63	241.00	40.73	60
0	—	—	—	230.87	33.17	60	230.30	40.66	54
5	232.74	36.74	65	232.19	33.86	63	228.76	40.65	63
10	233.05	31.62	61	225.17	37.99	65	234.60	35.90	60
15	245.84	32.41	63	223.80	34.41	61	239.64	50.68	66
20	244.55	32.95	58	—	—	—	244.92	43.45	65
25	246.64	29.52	59	243.79	41.43	58	243.94	40.45	66
30	255.67	38.51	61	240.00	37.62	59	253.18	49.92	61
35	268.55	36.67	58	267.08	47.85	61	258.82	50.60	61
<i>Auditory</i>									
-35	308.94	72.82	64	265.60	58.33	65	319.86	105.48	57
-30	301.83	73.60	59	264.96	72.89	71	352.62	119.89	71
-25	319.59	79.17	59	259.69	62.46	64	386.90	149.49	58
-20	311.73	78.62	60	263.09	74.58	70	—	—	—
-15	325.74	105.93	62	263.62	54.76	64	438.36	157.76	44
-10	368.21	102.97	58	272.74	61.53	70	325.02	108.08	55
-5	392.67	158.56	48	282.39	50.55	62	319.67	93.06	60
0	—	—	—	299.13	71.83	64	285.44	87.77	64
5	429.78	159.44	54	312.43	62.33	65	274.73	60.45	60
10	358.00	127.65	62	353.14	90.31	56	261.76	55.18	66
15	302.53	73.33	57	428.86	174.26	56	259.82	67.70	65
20	301.29	84.94	62	—	—	—	249.22	62.48	59
25	309.69	97.81	59	359.75	134.59	63	254.40	65.17	65
30	287.16	93.49	57	326.25	94.11	64	250.19	68.73	62
35	300.56	92.26	64	319.04	105.42	71	263.40	74.32	67

N, number of observations.

was detectable. To compare centrifugal vs centripetal saccade latencies the range considered was only from 5 to 15 deg of target displacement. For centrifugal saccades mTD was never > 15 deg and in the centripetal direction saccades > 20 deg become centrifugal. In the 5–15 deg range centrifugal latencies were about 20 msec longer than centripetal ones [ $F_{(1,731)} = 57.44$ ;  $P < 0.001$ ] without any interaction with mTD [ $F_{(2,731)} = 0.05$ ;  $P = 0.951$ ].

Finally, we compared centrifugal C20 saccades with C0 saccades which were only centrifugal. For mTD ranging from 5 to 15 deg, latencies were about 10 msec longer for C20 than for C0 [ $F_{(2,719)} = 7.33$ ,  $P = 0.001$  and no interaction with mTD  $F_{(4,719)} = 0.89$ ,  $P = 0.467$ ]. Figure 2(D) shows the mean latency vs target displacement in the three experimental conditions. Data for condition C – 20 have been represented vs target displacement-mirror.

In conclusion, the statistical analyses of the data shown in Fig. 2 demonstrate that visual response latency increases as target displacement increases and this is particularly true for large target displacement. We found the same trend for all starting positions although an additional constant bias of about 10 msec was detectable for C20.

### Auditory targets

Figure 3(A) shows the mean latency of primary saccades toward auditory targets recorded in condition C0. As already known from previous studies (Zahn *et al.*, 1978; Zambarbieri *et al.*, 1982; Jay & Sparks, 1990), the latency of the responses decreases, as the eccentricity of the auditory target increases.

Figure 3(B) shows the mean latency of auditory responses obtained in condition C + 20. The longer latencies which corresponded to target positions of  $\pm 5$  deg in condition C0, are now found for target positions of +15 and +25 deg, which correspond to a target displacement of  $\pm 5$  deg. A mirror-symmetrical diagram can be observed in Fig. 3(C) where the results obtained in condition C – 20 are reported.

In Fig. 3(D) latencies are plotted vs target displacement (data for condition C – 20 are plotted vs mTD). It is clear that latency mean values shifted according to initial eye position. For any fixation target, latency showed an opposite trend as compared with the visual case: the highest values corresponded to 5 deg target displacement and then steeply decreased when passing to 10 and 15 deg target displacement. Beyond this limit the latency decreased very smoothly. The latency differences between

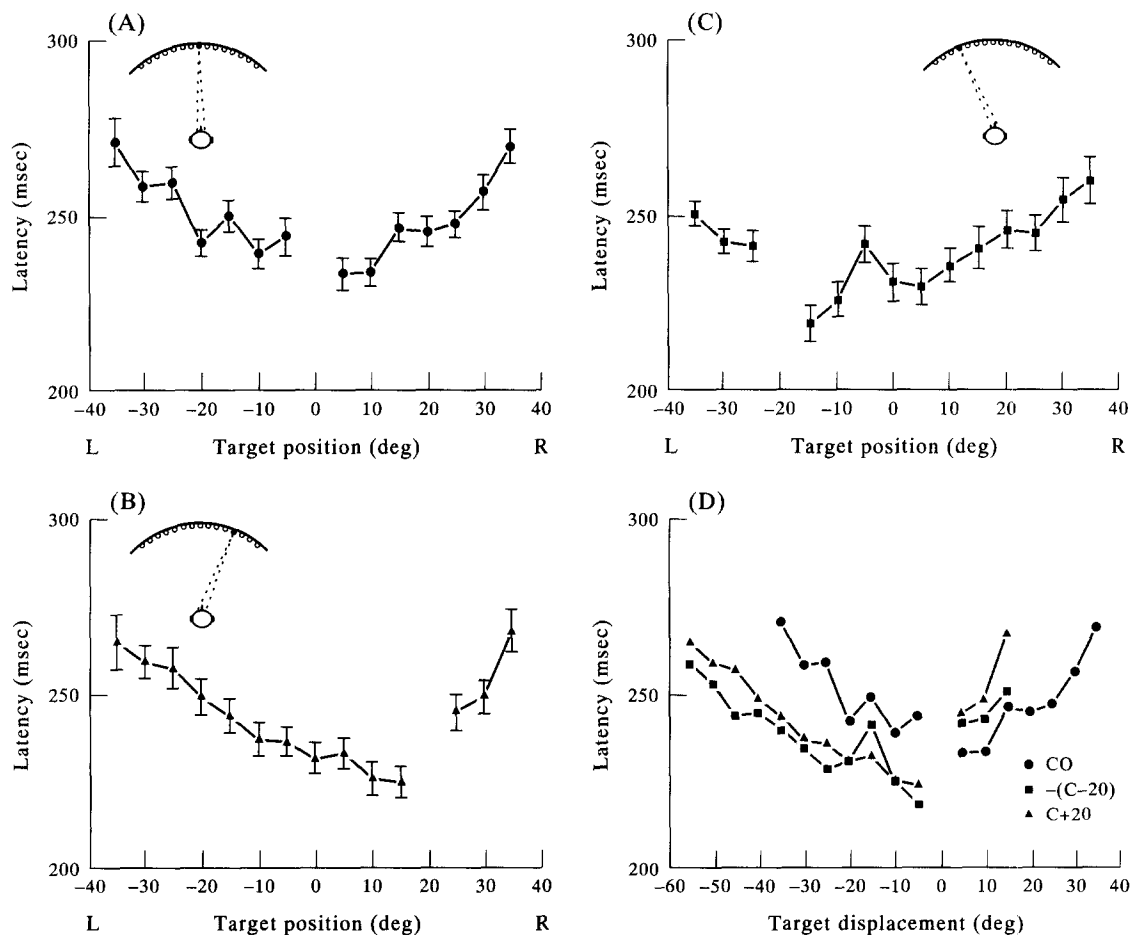


FIGURE 2. Mean latency of primary saccades evoked by visual target presentation with different initial positions of the eyes in the orbit. (A) The eyes were in the primary position; (B) the eyes were rotated 20 deg to the right; (C) the eyes were rotated 20 deg to the left; (D) the mean latency is plotted vs target displacement for condition C0 and C + 20. Results from condition C – 20 are plotted vs target displacement changed in sign. Vertical lines indicate the SE. For the sake of figure clarity the ordinate scale is different from that in Fig. 3.

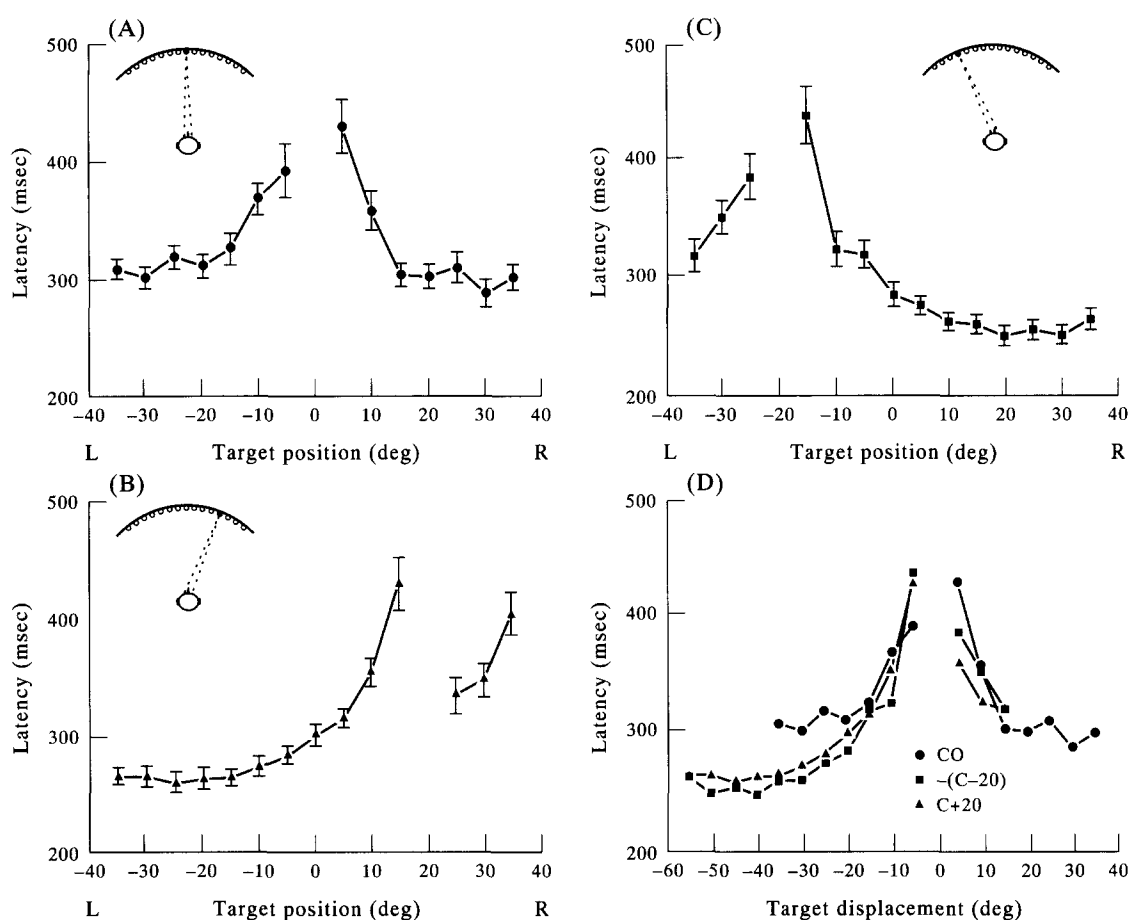


FIGURE 3. Mean latency of primary saccades evoked by auditory target presentation with different initial positions of the eyes in the orbit. Data as in Fig. 2.

visual and auditory responses is larger for the small target displacement (auditory greater than visual) and decrease as target displacement increases.

In the statistical analysis of the auditory responses we followed the same steps described for visual responses. As in the visual case, saccade direction proved not to be significant in the C0 condition either as a main effect [ $F_{(1,811)} = 0.63$ ;  $P = 0.428$ ] or in interaction with absolute target displacement [ $F_{(6,811)} = 0.95$ ;  $P = 0.497$ ] whereas absolute value target displacement was significant [ $F_{(6,811)} = 18.29$ ;  $P < 0.001$ ] showing the trend described above.

The mTD transformation showed that C - 20 and C + 20 were symmetrical with respect to target displacement [mTD,  $F_{(13,1730)} = 38.29$ ,  $P < 0.001$ ; FT,  $F_{(1,1730)} = 2.81$ ,  $P = 0.094$ ; FT\*mTD,  $F_{(13,1730)} = 0.89$ ,  $P = 0.566$ ]. The centrifugal-centripetal asymmetry was not detectable for auditory saccades [ $F_{(1,714)} = 4.41$ ,  $P = 0.036$ ]. However it is important to emphasize that for 5 deg target displacement, the centripetal-centrifugal difference was 60.28 (433.04 vs 372.76 msec), and only -0.912 (340.119 vs 339.207 msec) and -3.5 (319.406 vs 315.904 msec) for 10 and 15 deg respectively. Finally, C0 showed longer latencies than C20 [ $F_{(1,2046)} = 22.12$ ,  $P < 0.001$ ]; this was true for all target displacement (differences ranging from +12 msec for 5 deg to +43 msec for 35 deg) but for 20 deg (difference -3 msec).

In conclusion, the statistical analyses of the data shown in Fig. 3 suggest that auditory response latency decreases as target displacement increases, especially for small target displacement. This trend is the same for all starting positions although usually C0 shows longer latencies than C20.

## DISCUSSION

The experimental results reported in this paper clearly indicate that visual saccade latency depends on target displacement being longer for larger target displacement. In the wide range of target displacement considered the difference between minimum and maximum mean latency did not exceed 40 msec.

The same behaviour was reported in several studies that have examined the way in which saccade latency varies as a function of target eccentricity (Bartz, 1962; White, Eason & Bartlett, 1962; Becker & Jürgens, 1979; Sharpe, Lo & Rabinovitch, 1979; Kalesnykas & Hallett, 1994). Visual latency was almost constant when a narrow range of target displacements, not greater than 20 deg, was considered (Cohen & Ross, 1977; Heywood & Churcher, 1980; Findlay, 1983). In contrast, for very small retinal eccentricity of the target, not exceeding 4-5 deg, latency has been observed to decrease as a function of eccentricity (Wyman & Steinman, 1973; Kalesnykas & Hallett, 1994).

Also for saccades evoked by auditory target presentation, we found that the latency depends primarily on the position of the target with respect to the eyes. In the same range of target displacement in which visual latency increases, auditory saccade latency decreases as the target displacement increases. These findings agree with others reported in the literature (Zahn *et al.*, 1979; Jay & Sparks, 1990).

In addition, the total variation of latency between the minimum and the maximum target displacement is significantly longer than in the visual case. The rate of variation is not constant but presents a steep decay between 5 and 15 deg target displacement. Qualitatively this behaviour is similar to that observed for very small visual saccades (Wyman & Steinman, 1973; Kalesnykas & Hallett, 1994). In summary, both auditory and visual latencies are related to target displacement but in opposite directions.

Since the execution mechanism for both visual and auditory saccades is likely to be the same (Zambarbieri *et al.*, 1982; Jay & Sparks, 1987a), the origin of the observed behaviour in auditory responses has to be looked for at the level of the processing that produces the motor command for the saccadic mechanism.

The processing underlying the generation of a goal-directed saccade could be divided into three steps (Fig. 4). Step I represents the process of target localization which is based on the incoming sensory information. Step

II represents the central processing, likely to involve primarily the SC, which further elaborates target position coded in the reference frame of the relevant sensory system. Step III corresponds to the final transformation, from the position of the target to the motor command for the execution mechanism.

A variation in latency reflects a variation in the time required to execute a given process. If we make the assumption that the signal entering each one of these steps is affected by uncertainty, the time required to produce the output depends on the level of this uncertainty. Uncertainty can be imagined as a noise affecting the signal. The greater the noise, the longer the time required to reach a given level in the estimation process. By assuming a variable signal-to-noise ratio, the variation of latency can be easily predicted.

Which one of these steps could be responsible for the observed variation in auditory responses latency?

In a first study, dealing with the latency of auditory responses recorded in a condition comparable with condition C0 of the present experiments (target position and target displacement were identical), a stochastic model for the generation of saccadic responses was proposed and succeeded in simulating the latency behaviour detected in the experiment (Schmid, Magenes & Zambarbieri, 1982). The origin of the noise affecting the signal was supposed to be related to the process of sound localization in space, which is based on the differences in

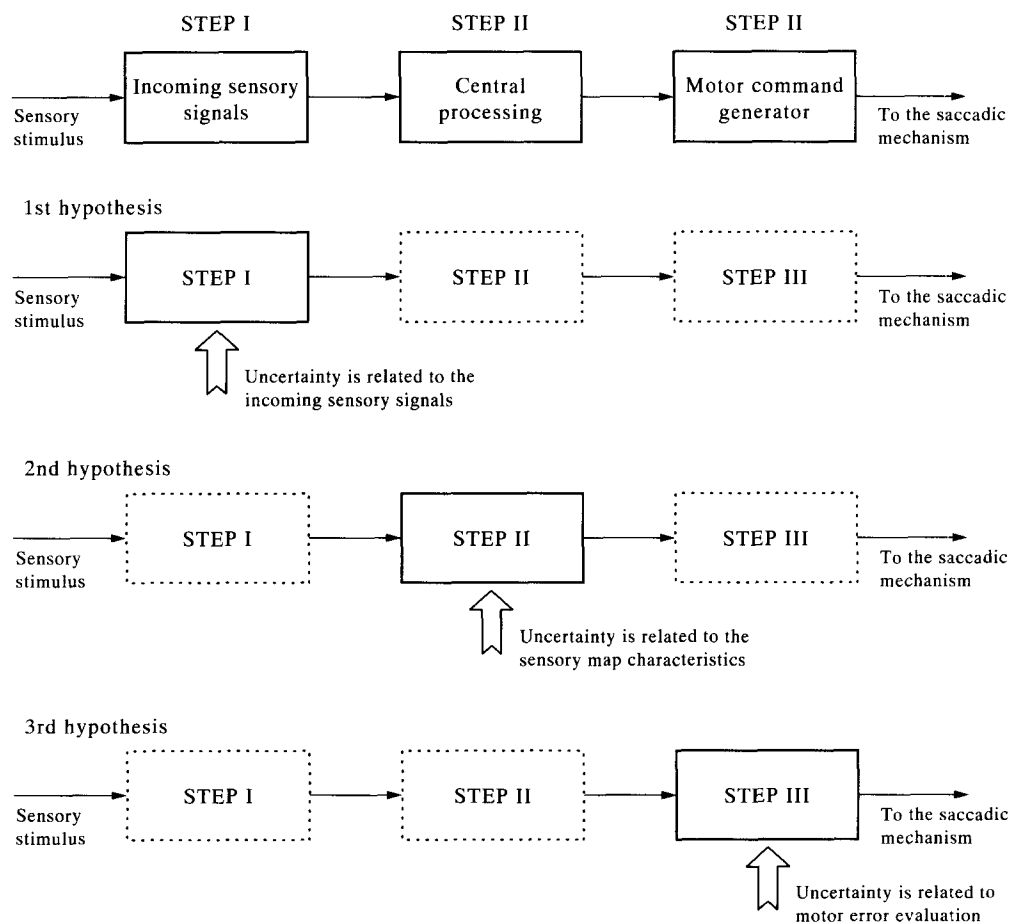


FIGURE 4. Schematic representation of the three steps involved in saccade generation and of the three hypotheses described in the Discussion.

the intensity and timing of the signals perceived by the two ears. Targets placed near the midline with respect to the head produce small differences and therefore they are likely to be associated with greater level of uncertainty and longer latencies as compared with more eccentric targets. Referring to Fig. 4, this hypothesis involves the first step as the source of uncertainty (1st hypothesis).

Our new experiments show that saccade latency depends on target displacement rather than on target position. Since target displacement derives from both target position and starting eye position in the orbit, the previous hypothesis of a noise affecting the incoming auditory information, thus considering target position only, cannot be considered as the only source of uncertainty.

Consider the results obtained by Jay and Sparks (1984, 1987b). They placed a monkey in front of an auditory target located 20 deg right and recorded the activity of SC neurons. The initial position of the eyes was changed from trial to trial. The same neuron that was strongly active when the eyes were initially 24 deg left, has a reduced activity when the eyes were in the primary position and did not respond at all when the eyes were 24 deg right. Therefore the receptive fields of neurons in the auditory map of the SC seems to be related to the position of the target with respect to the eyes (target displacement) or, as the authors stated "the auditory map shifts with changes in eye position". A similar shift was previously reported in SC quasi-visual cells (Sparks & Porter, 1983). In Jay and Sparks experiments the amount of auditory map shift was only 12.9 deg on average and did not match the 24 deg change in eye position.

Jay and Sparks' hypothesis deals with Step II: the auditory sensory map shifts according to the incoming starting eye position signal and is kept in register with the motor error retinotopic map of the SC. In this way any feature of the auditory map will also shift and will show up depending on target displacement rather than on target position. For instance, if the auditory map receptive fields have different levels of selectivity and need longer latencies to generate small saccades this idiosyncratic behaviour will be detected for target displacement requiring for small saccades, no matter what the location of the target. Different sensory modalities may correspond to different sensory maps with different features and different behaviour in accessing to a common motor map for saccade execution, as proved by visual and auditory latencies that show opposite relationships with target displacement. Since the output provided by this step in the form of motor error would be the same for visual and auditory target presentation, the same kind of signal processing is likely to be performed downstream to control the execution of the saccadic movement.

An alternative hypothesis, involving Step III (3rd hypothesis), could be suggested. If we assume that the signal provided by the two first steps represents target position with respect to the head, this signal has to be compared with a signal representing the actual eye position in the orbit in order to generate a motor error to

drive the burst units. Both signals are affected by uncertainty and in our auditory paradigm both signals are extraretinal. The uncertainty affecting target position is linked to the nature of sensory information. The uncertainty affecting eye position is increased as the visual input disappears when the auditory target appears. The level of noise affecting the signals is not necessarily position-dependent. The smaller the difference between the two signals the greater the effect of uncertainty on the process of motor error evaluation. In other words, the system may be reluctant to trigger saccades for motor error with an amplitude very close to the minimal resolution of the incoming sensory signal. This hypothesis is in keeping with the few auditory units represented among small motor error in the SC (Jay & Sparks, 1987b). Moreover, this could be the case also for visual saccade latency for very small target displacements, which is qualitatively similar to that of auditory saccades (Wyman & Steinman, 1973; Kalesnykas & Hallett, 1994).

In conclusion, after having excluded, on the basis of the experimental evidence (dependence of variation on target displacement), the first hypothesis (Step I) as the only source of latency variation, both of the other two hypotheses could be possible. The auditory map shift reported in the monkey by Jay and Sparks (1987b) strongly supports the second hypothesis (Step II). However, the third hypothesis cannot be excluded since the map shift did not completely correspond to the change in eye position and there may be some differences among species as suggested by Harris, Blakemore and Donaghy (1980) who failed to find a similar shift in the cat.

## REFERENCES

- Bartz, E. A. (1962). Eye-movement latency, duration, and angular response time as a function of angular displacement. *Journal of Experimental Psychology*, 64, 318-324.
- Becker, W. & Jürgens, R. (1979). An analysis of the saccadic system by means of double step stimuli. *Vision Research*, 19, 967-983.
- Cohen, M. E. & Ross, L. E. (1977). Saccade latency in children and adults: Effects of warning interval and target eccentricity. *Journal of Experimental Child Psychology*, 23, 539-549.
- Cynader, M. & Berman, N. (1972). Receptive-field organization of monkey superior colliculus. *Journal of Neurophysiology*, 35, 187-201.
- Findlay, J. M. (1983). Visual information processing for saccadic eye movements. In Hein, A. & Jeannerod, M. (Eds), *Spatially oriented behavior* (pp. 281-303). Berlin: Springer.
- Harris, L. R., Blakemore, B. & Donaghy, M. (1980). Integration of visual and auditory space in the mammalian superior colliculus. *Nature (London)*, 288, 56-59.
- Heywood, S. & Churcher, J. (1980). Structure of the visual array and saccade latency: Implications for oculomotor control. *Quarterly Journal of Experimental Psychology*, 32, 335-341.
- Hikosaka, O. & Wurtz, R. H. (1985). Modification of saccadic eye movements by GABA-related substances. I. Effects of muscimol and bicuculline in monkey superior colliculus. *Journal of Neurophysiology*, 53, 266-291.
- Jay, M. F. & Sparks, D. L. (1984). Auditory receptive fields in the primate superior colliculus that shifts with changes in eye positions. *Nature (London)*, 309, 345-347.
- Jay, M. F. & Sparks, D. L. (1987a). Sensorimotor integration in the primate superior colliculus. I. Motor convergence. *Journal of Neurophysiology*, 57, 22-34.

- Jay, M. F. & Sparks, D. L. (1987b). Sensorimotor integration in the primate superior colliculus. II. Coordinates of auditory signals. *Journal of Neurophysiology*, *57*, 35–55.
- Jay, M. F. & Sparks, D. L. (1990). Localization of auditory and visual targets for the initiation of saccadic eye movements. In Berkley, M. & Stebbins, W. (Eds), *Comparative perception. I. Basic mechanisms* (pp. 351–374). New York: Wiley.
- Kalesnykas, R. P. & Hallett, P.E. (1994). Retinal eccentricity and the latency of eye saccades. *Vision Research*, *34*, 517–531.
- Robinson, D. A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vision Research*, *12*, 1795–1808.
- Schiller, P. H. & Stryker, M. (1972). Single-unit recording and stimulation in superior colliculus in the alert rhesus monkey. *Journal of Neurophysiology*, *35*, 915–924.
- Schmid, R., Magenes, G. & Zambbarbieri, D. (1982). A stochastic model of central processing in the generation of fixation saccades. In Roucoux, A., & Crommelinck, M. (Eds), *Physiological and pathological aspects of eye movements* (pp. 301–311). The Hague: (W.) Junk.
- Sharpe, J. A., Lo, A. W. & Rabinovitch, H. E. (1979). Control of the saccadic and smooth pursuit systems after cerebral hemidecortication. *Brain*, *102*, 387–403.
- Sparks, D. L. & Mays, L. E. (1980). Movement fields of saccade-related burst neurons in the monkey superior colliculus. *Brain Research*, *190*, 39–50.
- Sparks, D. L. & Porter, J. D. (1983). Spatial localization of saccade targets. II. Activity of superior colliculus neurons preceding compensatory saccades. *Journal of Neurophysiology*, *49*, 64–74.
- White, C. T., Eason, R. G. & Bartlett, N. R. (1962). Latency and duration of eye movements in the horizontal plane. *Journal of the Optical Society of America*, *52*, 210–213.
- Wurtz, R. H. & Albano, J. E. (1980). Visual-motor function of the primate superior colliculus. *Annual Review of Neuroscience*, *3*, 189–226.
- Wurtz, R. H. & Goldberg, M. E. (1972). Activity of superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. *Journal of Neurophysiology*, *35*, 587–596.
- Wyman, D. & Steinman, R. M. (1973). Latency characteristics of small saccades. *Vision Research*, *13*, 2173–2176.
- Zahn, J. R., Abel, L. A. & Dell'Osso, L. F. (1978). Audio-ocular response characteristics. *Sensory Process*, *2*, 32–37.
- Zahn, J. R., Abel, L. A., Dell'Osso, L. F. & Daroff, R. B. (1979). The audio-ocular response: Intersensory delay. *Sensory Process*, *3*, 60–65.
- Zambbarbieri, D., Schmid, R., Magenes, G. & Prablanc, C. (1982). Saccadic responses evoked by the presentation of visual and auditory targets. *Experimental Brain Research*, *47*, 417–427.