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Internal representation of gaze direction with and without retinal inputs in man

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Abstract

The contribution of retinal and extraretinal signals to the coding of eye position in the head was studied in human subjects (Ss). Horizontal saccades were produced in darkness. For some trials, before returning gaze direction to the starting position, a visual signal briefly stimulated the foveal retina. Results showed that this retinal input helped Ss to perceive gaze orientation more accurately after the saccade suggesting that the internal representation of eye position was improved when both extraretinal and retinal signals were available.

Keywords: Eye position coding; Extraretinal; Retinal; Vision; Saccade; Space perception

The central nervous system (CNS) must be informed about the orientation of the eyes in the orbits in order to determine the location of visual targets in relation to the body. Two alternatives are that (a) the commands from the brain to the eye muscles (i.e. outflow theory) or (b) proprioception from the extraocular muscles (i.e. inflow theory) provide the basic information for coding gaze direction (see Ref. [4] for a review). However, more contemporary models for eye position coding incorporate both efferent and afferent information [4–6]. To date, most of the knowledge on the role of proprioception and efferent copy for registering gaze direction comes from experimental conditions that combine both retinal and extraretinal signals (e.g. [2,4–7,9,10]). However, results from different laboratories suggest that there is limited capacity for coding gaze direction when extraretinal signals are not coupled with retinal inputs (e.g. [3,8]). In the present experiments, we assessed whether the accuracy of the internal representation of eye position in the orbits is impaired when no retinal signals are available.

The S ($n = 5$) sat 85 cm in front of a black semicylindrical screen in a completely dark room. Horizontal eye position was monitored with the EOG method. A bite-board was used to stabilize the S's head. Fig. 1 presents the spatio-temporal organization of the trials. At the start of each trial, S fixed a LED target presented directly in front of him for 3 s. Following extinction of that target, the S was required to make a horizontal saccade of self-selected amplitude to the right and to hold the new position. In one series of trials (the retinal/extraretinal condition), a red laser spot appeared for 200 ms in the foveal region 800 ms after the saccade peak velocity was detected. The eye position signal was used online to direct, with a mirror mounted on a galvanometer, the visual spot such that it fell within the 2° visual angle subtended by the fovea (see Fig. 1 caption for details about the technique used). Because this visual signal was positioned on the fovea, it could not provide any direct cue about gaze direction after the saccade. Following the extinction of this brief visual signal, the S was asked to return his gaze to the starting position. At this time, the central fixation target was turned on again to help the S return his gaze straight ahead and stabilize eye position until the end of the trial. About 300 ms after gaze returned to the starting position, the laser spot reappeared randomly either at 4, 6, or 8° on either side of the position attained by the initial saccade. While visually fixating the central target, the S was required to position the spot using a press-button device, at the same location that he thought he had reached during the initial saccade.

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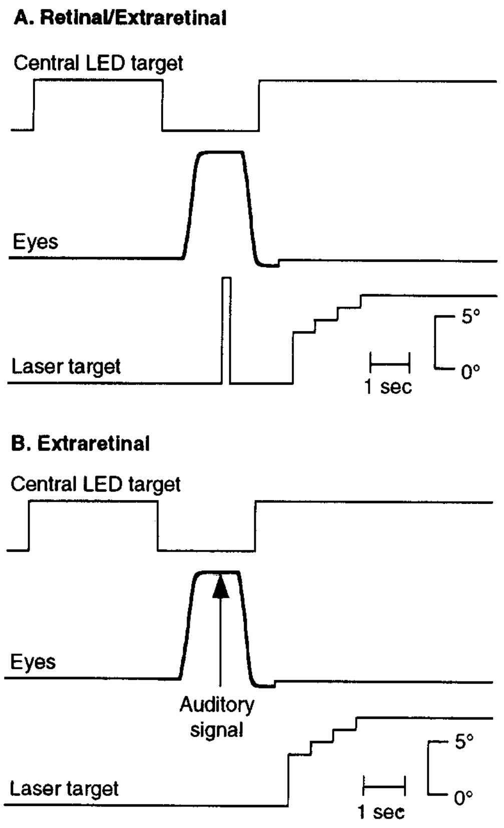

Fig. 1. Spatio-temporal organization of the trials in the retinal/extraretinal (A) and the extraretinal (B) conditions. In both conditions, the S produced a (self-selected amplitude) saccadic eye movement in complete darkness after the extinction of a central fixation target. Before returning gaze to the center position, either a brief laser spot was projected on the screen in such a position that it appeared in the foveal region (retinal/extraretinal condition) or a brief auditory signal coming from a fixed position behind the subject was given (extraretinal condition). Thus, the duration of gaze deviation after the initial saccade was similar in both conditions. After gaze returned to the central position, S fixated again the central fixation target. Then the laser spot reappeared randomly either at 4°, 6°, or 8° on either side of the position attained by the initial saccade. Using a press-button device, the S was required to position the spot at the same location that he thought he had reached during the initial saccade. The technique for projecting the laser spot was as follows: at the start of each trial, the EOG signal was averaged during 200 ms when the subject was gazing at the central target to measure the EOG drift. Then, 600 ms after peak velocity, that is when the eyes had reached a stationary position, the EOG signal was averaged during 200 ms to remove effects of noise in the EOG position signal. The actual gaze eccentricity was calculated by subtracting the EOG mean signal before from that obtained after the saccade. The measured position signal was then used to rotate a galvanometer-mounted mirror which projected a laser spot to the position fixated by the subject. This method proved to be accurate enough to provide the subject with the feeling that the target appeared at the point of fixation (i.e. within the 2° fovea).

In a second series of trials (the extraretinal condition), an auditory signal was given rather than a visual signal, 800 ms after the computer detected saccade peak velocity. This signal came from a fixed position behind the S and indicated to the S to bring gaze direction back to the center position. The other features and the spatiotemporal organization of the trials were identical to those described in the retinal/extraretinal condition. In particular, the duration of gaze deviation after the initial saccade was similar in both conditions. The S was instructed to cover most of the oculomotor range with his initial saccade in 50 trials. Trials showing eye drifts after the initial saccade were excluded from the analysis. The experiment was controlled by a personal computer equipped with a 12-bit A/D–D/A converter board. The EOG signal and the laser projection position were sampled at a rate of 100 Hz.

Simple linear regression analysis showed a high correlation (R^2) between the actual amplitude of the saccade and the S's perception of his eye deviation after the saccade in both conditions but, as shown in Table 1, R^2 coefficients were somewhat higher in the retinal/extraretinal (mean of 0.95) than in the extraretinal (mean of 0.90) conditions.

Because linear regression analyses do not provide information about accuracy *per se* but detail how well two variables are correlated, the angular difference between the actual and perceived saccade amplitude was also measured. Because most of the under- and overestimation errors were equally distributed across saccade amplitudes, the absolute errors gave a better representation of the results. As shown in Fig. 2, the absolute mean errors were smaller in the retinal/extraretinal than in the extraretinal condition ($F(1,4) = 62.36$, $P < 0.001$). Similar results were obtained for the relative absolute errors (i.e. ratio of absolute error magnitude to saccade amplitude, $F(1,4) = 16.31$, $P < 0.001$).

Overall, these results suggest that a more accurate internal representation of gaze direction (or better access to that representation) is available when extraretinal signals are combined with retinal inputs. This finding is of considerable importance because retinal signals are rarely considered in models of eye position coding. The question that arises, however, is how our foveal stimulus helped subjects to encode gaze direction more accurately despite the fact that it did not provide a fixed reference landmark. Neurophysiological studies have shown the existence of bimodal cells in the posterior parietal lobe, a key site for spatial representation, whose activity is modulated by both extraretinal and visual inputs [1]. Such

Table 1

Linear regression parameters representing subjects' perception of gaze orientation after the saccade

Ss	Retinal/extraretinal			Extraretinal		
	Slope	Intercept	R^2	Slope	Intercept	R^2
1	0.91	−1.27	0.97	0.96	−2.86	0.88
2	0.95	0.47	0.96	0.93	0.35	0.89
3	0.86	2.93	0.92	0.78	3.33	0.91
4	1.04	0.35	0.96	0.97	−0.78	0.91
5	1.04	−0.39	0.96	1.02	0.07	0.89

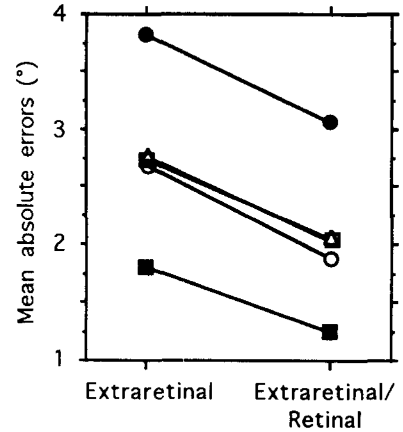

Fig. 2. Mean absolute angular difference (error) between actual and perceived saccade amplitude for the conditions with (extraretinal/retinal) and without (extraretinal) foveal stimulation after the saccade for each subject. The error decreased when the foveal region was briefly stimulated after the saccade produced in complete darkness.

bimodal cells might significantly contribute to the results we obtained. In conclusion, our results suggest that retinal inputs can be thought of as having a validation or a gating function that enables extraretinal signals to be further processed by the CNS, thus increasing the accuracy of the internal representation of gaze direction.

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