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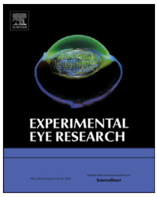

Source of high-frequency oscillations in oblique saccade trajectory

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ABSTRACT

Most common eye movements, oblique saccades, feature rapid velocity, precise amplitude, but curved trajectory that is variable from trial-to-trial. In addition to curvature and inter-trial variability, the oblique saccade trajectory also features high-frequency oscillations. A number of studies proposed the physiological basis of the curvature and inter-trial variability of the oblique saccade trajectory, but kinematic characteristics of high-frequency oscillations are yet to be examined. We measured such oscillations and compared their properties with orthogonal pure horizontal and pure vertical oscillations generated during pure vertical and pure horizontal saccades, respectively. We found that the frequency of oscillations during oblique saccades ranged between 15 and 40 Hz, consistent with the frequency of orthogonal saccadic oscillations during pure horizontal or pure vertical saccades. We also found that the amplitude of oblique saccade oscillations was larger than pure horizontal and pure vertical saccadic oscillations. These results suggest that the superimposed high-frequency sinusoidal oscillations upon the oblique saccade trajectory represent reverberations of disinhibited circuit of reciprocally innervated horizontal and vertical burst generators.

1. Introduction

Ideal ballistic movements have short transit time and straight trajectory. The trajectories of most common rapid eye movements, oblique saccades, are curved and irregular (Becker and Jurgens, 1990; King et al., 1986; Viviani et al., 1977). A number of studies have commented on the physiology of oblique saccades (Becker and Jurgens, 1990; Evinger and Fuchs, 1978; Guitton and Mandl, 1980; King et al., 1986; Smit et al., 1990; van Gisbergen et al., 1985; Weber et al., 2009). Visual-motor coordinate transformation and coupling between the output of horizontal and vertical burst generators (Becker and Jurgens, 1990; Grossman and Robinson, 1988), transient imbalance between yoked extra-ocular muscles and shifts in extra-ocular orbital pulleys (Weber et al., 2009), and decomposition of the oblique vector into its horizontal and vertical components at the level of motor neurons and the eye plant (Quaia and Optican, 1997) could produce oblique saccades with variable and curved path.

Trajectories of oblique saccades also have high frequency oscillations (Becker and Jurgens, 1990; Viviani et al., 1977). The speculated cause of such oscillations was cross-inhibition between horizontal and vertical saccadic burst generators (Becker and Jurgens, 1990; Grossman and Robinson, 1988). Becker and Jurgens (1990) suggested that the inequality in low-pass filtering of oscillations generated at horizontal and vertical saccadic burst generators can explain independent sources of oscillations evident in their experimental results.

Pure horizontal and vertical saccades cause high frequency oscillations along orthogonal axes (Ramat et al., 2005; Shaikh et al., 2007). Such oscillations are due to the inherent instability in the reciprocally inhibiting circuit of saccadic burst generators. These oscillations have distinct frequency ranging between 15 and 40 Hz (Ramat et al., 2005; Shaikh et al., 2007). We hypothesize that the activation of both horizontal and vertical burst generators during oblique saccades cause reverberations in these inherently unstable circuits. Such reverberations lead to high frequency oscillations of oblique saccade trajectory. In order to test this hypothesis, we first assessed whether the frequency of oscillations in oblique saccade trajectories falls in the same range as that of saccadic oscillations. Then we asked whether the frequencies of horizontal and vertical components of the oscillations during oblique saccades in a given individual are comparable to the frequencies of horizontal and vertical (orthogonal) oscillations during pure vertical and pure horizontal saccades in the same subject.

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2. Methods

Ten healthy subjects participated in the study. The subjects gave written informed consent. Cleveland Clinic institutional review board approved the experiment protocol. The age of participants was 29 ± 3 years. All the participants were with a refractive error of -4 ± 2 Diopters, but refractive error was corrected to normal with appropriate strength of contact lens.

2.1. Eye movement recordings

Video-based eye tracker (EyeLink 1000®, SR Research, Ontario, Canada) was used to measure horizontal and vertical eye positions while the subjects viewed a target projected on the LCD screen. A chin-rest provided head support. The head was 55 cm away from the LCD screen. Positions of both eyes were measured at 500 Hz temporal resolution. In off-shelf configuration, the EyeLink 1000® has an accuracy of 0.25° and resolution of 0.01° RMS. The difference in the digital output from EyeLink® during straight ahead gaze position and known eccentric gaze position, linear distance between two target locations on the screen, and distance between the screen and the subject's nasion were used to measure angular eye position. Further analysis was done off line on calibrated eye position vectors.

2.2. Experimental paradigm

Each subject followed a visual target projected on the LCD screen. In each trial, the target first appeared at straight-ahead position then shifted to the test location and back to straight-ahead position. Thus, each test location comprised of a set of saccade, one from straight-ahead to test location and vice versa. The test locations were 5°, 10°, and 15° to the right and left; 5° and 10° up and down, and in oblique directions (combinations of 10° to the right or left and up or down). Each subject did two identical trials, hence making 72 visually guided saccades (24 horizontal, 16 vertical, and 32 oblique). Our goal was to assess the frequency of orthogonal oscillations during saccadic eye movements. The oscillation frequency is determined by the state of the inherent instability of reciprocally innervating circuit of burst neurons and not the amplitude of the visually guided saccade (Shaikh et al., 2007, 2008). Therefore, in subsequent analysis we sorted saccades according to orientation of their trajectories (i.e. horizontal, vertical, and oblique).

2.3. Data analysis

Saccadic eye movements were identified with Engbert algorithm (Engbert and Mergenthaler, 2006). Epochs of eye positions that comprised saccades were used for further analysis. Saccade amplitude was the absolute difference between the eye positions at the start and the end of the saccade. To measure saccade velocity, all the eye positions epochs comprising of saccades were differentiated and smoothened with Savitzky–Golay filter (frame length: 21). To measure the acceleration, the eye velocity was further differentiated and smoothened with Savitzky–Golay filter (frame length: 21). Pure horizontal, pure vertical and oblique saccades were analyzed separately. Horizontal and vertical components of each saccade were analyzed independently. The inflections in the two-dimensional path of the eyes were measured in the phase-plane analysis. Custom written Matlab® programs were used for quantitative analysis of the phase-planes. Oscillations in the saccadic trajectories were analyzed in the acceleration trace; cycle-by-cycle analysis was performed for such purpose. Acceleration data was de-trended and realigned along the abscissa such that the peaks of the cycles remained positive and the troughs negative. The 'x' co-ordinate of the intersection of the data trace, moving from a negative value to a positive value, with the abscissa was recorded. The x-coordinate of the first data point that crosses the abscissa marked the beginning and the subsequent data point marked the end of a given cycle. The difference between two adjacent 'x' coordinates gave cycle width, and its inverse value gave cycle frequency. The difference between peak and trough measures corresponded to cycle amplitude.

3. Results

Fig. 1A, D and G illustrate pure horizontal saccade. Pure vertical saccade is shown in Fig. 1B, E and H. An example of the oblique saccade is depicted in Fig. 1C, F and I. Pure horizontal and pure vertical saccades have minimal inflections of their path (Fig. 1A and B). Such regularity is evident in smooth pulse of eye velocity signal (Fig. 1D and E) and biphasic acceleration trace (Fig. 1G and H). The trajectory of oblique saccade features marked inflections, which are more pronounced in velocity and acceleration traces (black arrows, Fig. 1C, F and I). These inflections of the oblique saccade trajectory appeared sinusoidal as if the oscillations were superimposed upon the saccade. Subsequent sections will describe the quantitative assessment of saccadic irregularity and sinusoidal oscillations.

Relationship of saccade velocity and amplitude gave elliptical phase-plane. The saccade amplitude determined the size of the ellipse. We analyzed phase-planes with the velocities and accelerations normalized to their corresponding peaks in order to compare inter-saccadic variability of inflections. Fig. 2 illustrates ellipses derived by plotting normalized velocities and normalized accelerations from multiple saccades from the same subject. Normalized ellipses from all horizontal saccades from a given subject are superimposed in Fig. 2A. Fig. 2B illustrates superimposed normalized ellipses representing all vertical saccades whereas Fig. 2C represents all oblique saccades. Amount of irregularity in a given saccadic trajectory was measured by fitting an elliptical function to the normalized phase-plane plot. The value of squared sum of error was computed for all elliptical fits. The average value of the sum of squared errors (mSSE; sum of squared error/number of saccades) was derived for each subject individually for pure horizontal, pure vertical and oblique saccades. Larger mSSE suggested larger deflections in the two-dimensional path of the saccade. In the example depicted in Fig. 2A–C, the values of mSSE for pure horizontal and vertical saccade were 0.0008 and 0.002, respectively. The value of mSSE further increased to 0.004 when the same subject made oblique saccades. The increase was statistically significant with one-way ANOVA ($p < 0.0001$). The trend of increasing irregularity, as evident by higher values of mSSE for oblique saccades, as compared to vertical and horizontal saccades was consistent amongst most subjects. Such trend was evident in the summary from all ten subjects depicted in Fig. 2D. The average value of mSSE for oblique saccades from all ten subjects was 0.005 ± 0.002, for vertical saccades it was 0.0035 ± 0.0015, and it was 0.002 ± 0.001 for horizontal saccades.

The inflections in two-dimensional path of the oblique saccades were often sinusoidal. Such high-frequency oscillations were prominent in both vertical and horizontal axes (Fig. 3A and B). Such oscillations were also seen in the composite vector for horizontal and vertical components comprising the oblique saccade pulse (Fig. 3C). During pure horizontal saccades, the oscillations were small and were seen only along the vertical (orthogonal) direction (Fig. 3D notice the difference in scale on y-axis). The pulse of horizontal eye velocity and the composite vector of horizontal and vertical eye velocity was smooth and regular (Fig. 3E and F). Likewise, horizontal oscillations were small and were present during