Space-time dependence of fixational saccades
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**Introduction**
We have recently shown that, in high-acuity tasks, microsaccades precisely relocate gaze toward nearby regions of interest (Ko et al., 2010). An important open question is why microsaccades also occur during fixation on an isolated marker in the absence of other visual stimuli. These fixational saccades cannot serve an explorative function. Two main theories have been proposed:

**Spatial theory:** Cornsweet (1956) first proposed that fixational saccades may correct for fixation errors. According to this view, fixational saccades are triggered by spatial displacements between the current gaze position and the fixation marker.

**Temporal theory:** Nachmias (1959) first proposed that the generation of fixational saccades is primarily determined by temporal factors. He argued that the duration of the inter-saccadic interval is the best predictor of saccade occurrence. These two theories have never been fully tested, primarily because of technical limitations. Here, we relied on our recent improvements in localizing the position of the preferred retinal locus of fixation to examine the spatial and temporal factors involved in the generation of fixational saccades.

**Methods**
Eye movements were recorded by means of a Generation 6 Dual Purkinje image eye-tracking system. Six observers maintained fixation on a high contrast small fixation marker (\(4^\circ\)) for 10 seconds in complete darkness. No other stimulus was present.

**A critical problem: Precise gaze localization**

Because of fixational eye movements, the standard calibration procedures routinely used in ocular motor research do not enable precise localization of the position of the center of the preferred retinal locus of fixation (PRFL). The region of uncertainty in localizing the PRFL is as large as the area of fixational instability, the area we want to resolve.

**Our approach: A gaze-contingent procedure**

In our procedure, observers refined the voltage-to-pixel mapping given by a preliminary standard calibration by correcting the position of a retinally-stabilized cross displayed at the estimated center of gaze. This gaze-contingent procedure decreased the dispersion of the gaze position by approximately a factor of 3 on each axis. This procedure was repeated frequently during the course of the experiment.

**Results**

**Spatial and temporal factors in the generation of fixational saccades**
Most fixational saccades were generated when the gaze position was very close to the fixation marker, the region in which the PRFL was most likely to be found. These saccades were not compensatory, as fixation errors were already minimal at the time saccades occurred.

The saccade rate, i.e., the number of fixational saccades occurring around a given eccentricity divided by the time spent at that eccentricity, increased with the fixation error.

As the fixation error increased, fixational saccades were increasingly more likely to reduce the spatial offset on the retina.

The rate of non-compensatory fixational saccades (fixational saccades that did not reduce the retinal offset) remained approximately constant with the fixation error.

The mean rate of fixational saccades was 1.3 ± 0.75 saccades/s. On average across observers, the median ISI was 693 ± 546 ms.

The distribution of intersaccadic intervals (ISI) changed with the fixation error present at the time of saccade occurrence. The closer was the PRFL to the marker, the longer was the ISI. These data show that temporal factors play an important role in the generation of fixational saccades.

Saccades occur even when the PRFL is close to the target, but only after longer delays.

**Corrective function of fixational saccades**
On average, fixational saccades were very accurate in correcting for fixation errors, an effect more pronounced on the horizontal axis than on the vertical one.

While centered on the correct average value, the distribution of displacements caused by fixational saccades possessed a relatively large standard deviation, which was little affected by the fixation error at the time of saccade onset.

Similar results were also obtained by examining errors on the axes parallel and orthogonal to the fixation offset present at the time of saccade occurrence: fixational saccades were on average very accurate in correcting for fixational displacements.

**Conclusions**
We used a gaze-contingent procedure for precisely localizing the line of sight in the scene. Our results show that the generation of fixational saccades depends on both spatial and temporal factors.

**Spatial factors:** Fixational saccades serve a corrective function. For any given fixation error, the spatial displacements resulting from fixational saccades form a broad distribution with average value very close to the displacement needed for perfect correction.

**Temporal factors:** Fixational saccades occasionally occur even when the center of gaze is very close to the fixation marker and saccades are not needed for correcting retinal offsets. These saccades, however, occur after longer intervals, as if a saccade can only be suppressed for a limited amount of time.

**References**

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