scientific reports

OPEN

Unstable foveation's impact on reading, object tracking, and its implications for diagnosing and intervening in reading difficulties

Niloufar Chamani, Michael Christoph Schmid✉ & Samy Rima

Foveation, the ability to focus on a point for clear vision, is crucial for reading smoothly and tracking moving objects. Research shows that unstable foveation disrupts reading by causing more frequent eye movements. However, it's unclear if this also affects smooth tracking of moving targets in slow readers. This study therefore investigates the link between foveation during reading and the tracking of moving targets, in a large group of participants displaying variable reading speeds in a virtual reality environment. Our analysis shows that slower readers have more intrusive fixational eye movements characterized by greater spatial and temporal variability during reading. Additionally, these readers display less efficient tracking of moving targets. Interestingly, the rate and spatial variability of catch-up saccades during object tracking correlates with fixational eye movement rates and spatial variability during reading. Our findings thus demonstrate that poor foveation stability in slow readers also affects other eye movement activities, such as during object tracking. We conclude with a discussion on the limitations of virtual reality-based reading assessment and the shared mechanisms of foveal stabilization, which might be altered under conditions of reading impairment.

Keywords Smooth pursuit eye movements, Reading fluency, Oculomotor control, Microsaccades, Saccadic inhibition, Fixational stability

Ocular fixation, or foveation, is the intricate neurological regulation of eye movements that allows the processing of stimuli with high spatial resolution[1]. Disruptions in foveation can lead to frequent, intrusive eye movements, negatively affecting reading speed and efficiency[2–4]. As such foveation is a hallmark of reading, but also more generally crucial for both static and dynamic visual stimulus processing. However, it is currently unclear whether limitations in foveation during one type of task generalize to other foveation needs.

During foveation, the eyes are never completely still and display a range of ocular motion classes. These include drifts, where the fovea glides around the prioritized stimulus with defined speeds and amplitudes. Tremors are small, involuntary, rhythmic oscillations that occur even when trying to keep the eyes still. There is currently no consensus on the origins or the function of ocular tremors. Fixational eye movements, including microsaccades, are small and rapid movements that refresh the retinal image, preventing visual fading[5]. Microsaccades correct drift overshoots and deploy attention to the periphery without losing sight of foveated objects[6–8]. They are predominantly binocular, biased toward horizontal movements, occurring 1–3 times per second and lasting between 6 and 30 milliseconds. Compared to tremors and drifts, microsaccades have higher velocities, averaging between 6 and 120 degrees per second, and larger amplitudes, up to 1 degree of visual angle[9].

The firing of neurons in the superior colliculus is under stringent control from omnipause neurons, a control that is crucial for the maintenance of fixation stability[10–12]. During text reading, foveation ensures sharp central vision by maintaining precise focus on individual words. Microsaccades play a crucial role by correcting drift overshoots and refreshing the retinal image, preventing visual fading and maintaining text clarity. The stochastic nature of neuronal activity, characterized by random and probabilistic occurrences, enhances this process by providing adaptability and flexibility, allowing the visual system to respond effectively to varying visual information sampling demands and preventing repetitive strain[13]. For reading, this adaptability of oculomotor control neurons aids in encoding by correcting saccadic landing errors and enabling regressive movements over nearby words[4,14,15].

Department of Neuro- and Movement Sciences, Faculty of Science and Medicine, University of Fribourg, Fribourg, Switzerland. ✉email: michael.schmid@unifr.ch

Previous research has shown that an increased number of microsaccades during reading correlates with slower reading speeds[2,4]. The failure to adapt microsaccade rates for reading needs can disrupt ongoing visual processing through saccadic suppression. This disruption can force a restart in the encoding of visual information[16,17]. Such difficulty in smoothly tracking text can hinder the transformation of text into phonemes and the extraction of lexical information, thereby further disrupting reading flow[14]. The result of this inefficient text encoding can translate to more frequent regular saccades to compensate for the information loss, and higher cognitive load, causing ocular and mental fatigue. Consequently, poor visual stability and increased cognitive effort result in slower reading speeds and reduced reading efficiency.

Beyond its necessity for proper reading, stable foveation is critical for smoothly pursuing moving targets. The ability to follow moving objects with the eyes is a key oculomotor function requiring the combined action of stable foveation and fine-tuned motion perception. Smooth ocular pursuit keeps an object in the central, most sensitive part of the visual field and is a prerequisite for object interception, avoidance, and navigation planning[18,19]. Key metrics of ocular smooth pursuit include gain, latency, catch-up saccades, tracking accuracy, and smooth pursuit duration. Gain is the ratio of eye velocity to target velocity, with a gain of 1 indicating perfect tracking[20,21]. Latency is the time delay between the onset of target movement and the initiation of eye movement, with shorter latencies indicating more responsive tracking[22]. Catch-up saccades are quick, corrective eye movements made to re-align the gaze with the moving target[18]; a higher frequency of catch-up saccades indicates less accurate smooth pursuit[23,24]. Tracking accuracy measures how closely the eye remains on the target, often calculated as the position error between target and eye positions[25]. Smooth pursuit duration reflects how long the eyes can maintain pursuit without needing catch-up saccades, with longer durations indicating more stable tracking[26].

In comparison to the study of eye movements during reading, very little is known about how eye movement abnormalities during smooth pursuit might affect reading. Black, Collins et al. (1984) demonstrated that a significant portion of poor-reading children show an increased number of saccades during smooth pursuit, suggesting that tracking abnormalities may contribute to reading difficulties[27]. Similarly, a study on a large cohort of children demonstrated that smooth pursuit eye movements in preschool children are strongly associated with phonological awareness, a key ability in reading acquisition. These findings suggest that early oculomotor skills play a crucial role in developing reading abilities[28]. Consistent with this interpretation, Judge, Caravolas, and Knox (2006) found that adults with dyslexia exhibit not only phonological difficulties but also smooth pursuit impairments, indicating that the relationship between these eye movements and reading skills persists into adulthood[29]. However, eye movements during reading were not assessed and therefore the relationship between saccades during reading and smooth pursuit remains unknown. Moreover, it remains to be clarified whether eye movement similarities between smooth pursuit and reading can be identified in regular readers.

The goal of this study is therefore to fill this knowledge gap by investigating fixational eye movement patterns across reading and ocular smooth pursuit within a large cohort of adult regular readers.

Methods

Study design and participants

This study utilized a dataset originally collected by Lohr, Aziz et al.[30], focusing on eye movements observed during reading and pursuit eye movement (PUR) tasks. In the original study, it was declared: ”Participants were recruited from the undergraduate student population at Texas State University in San Marcos, TX, USA. All participants were screened to ensure they had no history of epilepsy or seizures, and they all provided informed consent to participate in the study and to have their anonymized data shared with the broader research community following a protocol approved by the Institutional Review Board at Texas State University”. All methods were performed in accordance with the relevant guidelines and regulations. Data were collected longitudinally using the ET-HMD, a virtual reality head-mounted display (HMD) with integrated eye-tracking capabilities, based on the HTC Vive. The ET-HMD operates at a sampling rate of 250 Hz for eye-tracking and a display refresh rate of 90 Hz, providing a spatial accuracy of 0.2 degree of visual angle (dva). The participant group comprised 407 college students from Texas State University, with data collection spanning 26 months. Among these participants, 188 identified as male, 216 as female, and 3 as non-binary. All participants were native English speakers, and some had corrected vision using glasses or contact lenses.

Task description

Two specific tasks were focused on: Reading and smooth pursuit (PUR). The Reading task involved presenting text excerpts to participants, approximately 820 characters long, from a National Geographic article. The text was shown in a fixed-width black font on a light-gray background. It appeared within a viewing area of 51.2 × 37.6 dva at 0.6 m. Participants signalled completion via a button press. The PUR task required participants to follow with their gaze a black sphere, 0.5 dva in diameter, positioned at a depth of 1 m. The sphere moved horizontally on the screen at speeds of 5, 10, and 20 dva per second. It smoothly traversed between the left and right edges of the viewing region, which spanned ± 15 dva, pausing at random intervals at the edges before moving again. Participants completed these tasks up to a maximum of six times over three recording rounds, with each round comprising two recording sessions, contributing to a longitudinal dataset. For the reading task, different text excerpts were used: one for session 1 of Round 1, one for session 2 of Round 1, one for session 1 of Rounds 2 and 3, and one for session 2 of Rounds 2 and 3.

Preprocessing and analysis

All data analysis was performed using MATLAB Version 9.13 (R2022b) and R Version 4.4.0. The positions of the left and right eyes in head-centric coordinates were used, with the variables lx, ly, rx, and ry representing the horizontal and vertical positions of the left and right eyes, respectively. Since participants' heads were stabilized using a chin rest during data collection, the data predominantly reflect eye movements, with minimal contribution from head movements. To preprocess the data, a moving mean filter with a window size of 100 samples was applied to both the horizontal and vertical eye position signals of each eye using the `**fillmissing**` function in MATLAB. This function was used to handle missing data by smoothing the signals and providing a continuous dataset for further analysis. The mean positions for horizontal and vertical eye movements were calculated by averaging the processed signals from each eye separately for horizontal and vertical data (Fig. 1a). Initially, the study involved 407 subjects, but 10 were excluded due to significant data artifacts, and an additional 2 were removed due to missing data across key variables. After these exclusions, the final dataset for analysis comprised 395 subjects.

Task-specific analysis

Reading task

The 'Duration' metric for the reading tasks was normalized across participants using Z-scores to account for variability introduced by the use of four different reading texts during data collection. The analysis of the reading task focused on various metrics, including the mean fixation duration, microsaccades per second, spatial entropy and temporal entropy of microsaccades, ratio of regressive saccades to total saccades, mean amplitude of regressive saccades, rate of progressive saccades per second, and mean amplitude of progressive saccades. For detecting saccades, the method described by Engbert & Kliegl (2003) was used[7]. This method extracts saccades from raw eye position data by computing eye movement velocity and applying a threshold. Specifically, a velocity threshold of 6 times the median velocity was utilized to detect saccades. Additionally, the time span around the current sample used to compute the velocity was set to 20 ms, with the minimum duration for a saccade being 10 ms and the minimum separation time between two saccades being 12 ms.

Furthermore, to distinguish between saccades and microsaccades, we examined the amplitudes of identified eye movements. Microsaccades, featuring amplitudes less than 1 dva, were differentiated from larger saccades, which fell within the range of 1 to 15 degrees (Fig. 1b).

In addition to the initial filtering steps, further processing was conducted specifically for the saccades. This included the calculation of additional parameters such as the average velocity and the ratio of average velocity to peak velocity for each saccade. Filtering criteria were applied to refine the saccade dataset. Saccades with peak velocities exceeding 800 degrees per second, durations longer than 60 milliseconds or shorter than 10 milliseconds, and those with a ratio of average velocity to peak velocity falling outside the range of 0.3 to 2 were excluded from further analysis. Microsaccades were filtered by selecting those with an amplitude between 0.2 and 1 degree, and with an average-to-peak velocity ratio between 0.3 and 2 (Fig. 1d).

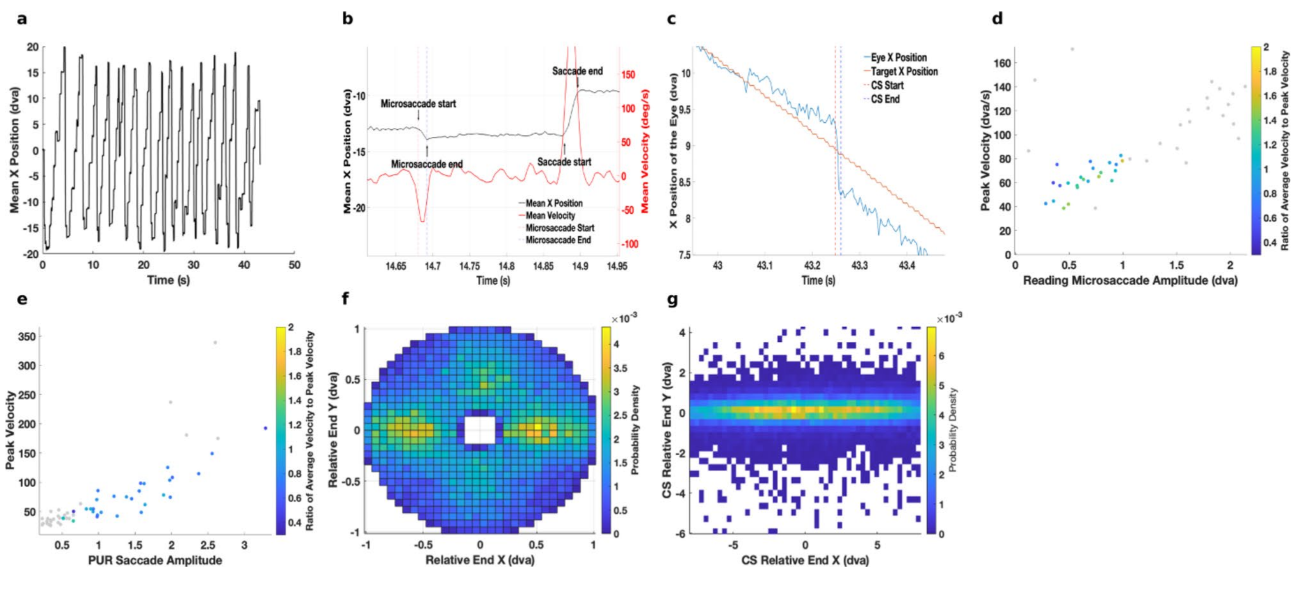

Fig. 1. Overview of eye movement trajectories and characteristics across reading and PUR tasks **(a)** an example of a reading trajectory showing the mean x-position between the right and left eye gaze, **(b)** an example of detected microsaccades, during reading. Microsaccades were included if their amplitude was between 0.2 and 1 dva, and their velocity surpassed 6 times the median velocity, **(c)** an example of detected catch-up saccade (CS) during PUR task performance, **(d)** example of included microsaccades, displaying the expected relationship between amplitude and velocity (main sequence) during reading from one subject. Gray dots represent data points that were filtered out, **(e)** example of included catch-up saccades during PUR from one subject. Gray dots represent data points that were filtered out, **(f)** landing point distribution for the microsaccades detected in the reading task, and **(g)** landing point distribution for the catch-up saccades detected in the PUR task.

In this study, both spatial and temporal entropy are quantified using Shannon's entropy formula[31], a fundamental concept from information theory that measures the amount of uncertainty or randomness in a dataset. For each microsaccade, the relative endpoint was determined by normalizing the initial x and y positions to (0,0) to provide all microsaccades with the same origin. To assess spatial entropy, a two-dimensional histogram with 100 bins is created for the x and y coordinates of microsaccade landing points during reading. Each bin represents the probability of a microsaccade landing within that spatial area relative to its origin. The entropy for this distribution is then calculated to quantify the spatial randomness of landing points. Specifically, entropy calculation involves generating histograms for each combination of conditions and normalizing the resulting images to obtain the entropy value. Figure 1f shows the landing point distribution for the microsaccades detected in the reading task.

To assess temporal entropy, latencies between consecutive microsaccades were used to form a probability density function, ensuring that the sum of all probabilities equals one. The entropy of these latencies was then calculated to evaluate the unpredictability in the timing of eye movements. By focusing only on non-zero probabilities, undefined values in calculations were avoided. The Shannon entropy formula was applied to provide a measure of entropy in bits. Each bit of entropy represents the expected amount of information or 'surprise' inherent in observing a particular event or state within the distribution. Higher entropy values indicate greater unpredictability or randomness in both spatial fixations and temporal latencies of eye movements within the dataset.

Smooth pursuit analysis

Catch-up saccade detection during the smooth pursuit was performed using the same velocity-based algorithm that was used for reading data[7] (Fig. 1c). A velocity threshold of 4 times the median velocity was applied to detect catch-up saccades. After detecting the catch-up saccades, the velocity was derived using the mean x-position of the eyes, to analyze the data during the sustained phase of smooth pursuit. A moving average filter with a window size of 200 samples was subsequently applied to the velocity data. Velocity thresholds were determined by identifying the maximum velocity within each trial and setting a threshold just below this peak. Velocities surpassing these thresholds were used to identify the sustained phases, ensuring dynamic consideration of different velocity ranges. This step was solely for detecting the start and end points of the sustained phase in each trial, as catch-up saccades had already been detected before applying these filters. During each sustained phase, the gain was calculated as the mean eye velocity divided by the corresponding target speed, accounting for eye movement direction. Catch-up saccades were included in this calculation and were not interpolated, allowing for the assessment of overall tracking effort. Velocity error was then determined as the deviation of the absolute pursuit gain from one, where positive values indicated that the eye was moving slower than the target, and negative values indicated that the eye exceeded the target speed. Position error was calculated as the difference between the eye position and the target position, where positive values indicated that the eye was ahead of the target. Catch-up saccades were excluded from the position error calculation to focus on steady-state tracking performance. For each subject and each speed condition, average values of gain and position error across trials were calculated.

Catch-up saccades were filtered according to several criteria: those with peak velocities over 800 degrees per second, amplitudes greater than 14 degrees or less than 0.5 degrees, durations outside the range of 10 to 60 milliseconds, and ratios of average velocity to peak velocity falling outside 0.3 to 2, were excluded from the analysis (Fig. 1e). Spatial entropy of these catch-up saccades was then quantified using the same method used to assess microsaccade landing point entropy during reading. For each catch-up saccade, the endpoint was calculated relative to its starting position, with the starting x and y coordinates normalized to (0,0). Figure 1g shows the landing point distribution for the catch-up saccades detected in the smooth pursuit task.

Statistical analysis

Before proceeding with the statistical analysis of the dataset, the mean of the parameters across all recorded instances for each subject was computed. This approach consolidated the data, creating a singular representative dataset per subject.

To explore the relationships between reading duration and various reading parameters, correlation analysis was performed. The correlation coefficient, p-value, and 95% confidence interval for each reading parameter's relationship with the Z-score of reading duration were calculated using the `**psych**` package in R.

The Generalized Additive Model (GAM), implemented in the `**mgcv**` package in R, was employed to capture the nonlinear relationships among the various reading parameters. This approach, an extension of general linear mixed models, replaces the assumption of linearity with smooth functions of the covariates[32]. The model was defined within the `**mgcv**` framework to include both smooth and linear terms. Smooth terms were used for variables such as mean fixation duration, microsaccades per second, spatial entropy, temporal entropy, mean amplitude of regressive saccades, and progressive saccades per second, allowing for modeling of intricate nonlinear dependencies. Linear terms were applied to the ratio of regressive saccades to total saccades and the mean amplitude of progressive saccades, because preliminary analysis showed that their relationships with reading duration were linear. Following model fitting, a thorough analysis of its performance was conducted, including the calculation of Root Mean Square Error (RMSE) to evaluate predictive accuracy. The RMSE was contextualized by comparing it to the standard deviation of the dependent variable, reading duration, to assess relative accuracy[33]. To further investigate reading behaviors, a two-tailed t-test with an alpha level of 0.05 was conducted to compare individuals with a reading duration 2 standard deviations higher than the mean (slow readers) to the general population. The variables compared were microsaccade rate, spatial entropy, and temporal entropy. For the PUR data, a statistical comparison of conditions for different speed and direction combinations was conducted using a two-way ANOVA in MATLAB. This analysis aimed to determine the effects on the rate of catch-up saccades, position error, and velocity error. The comparisons of interest were speed (5, 10, 20) and direction (left, right). Post-hoc analyses were performed using Tukey's HSD test. Boxplots with notches were used to display 95% confidence intervals for the medians, with error bars representing the standard error of the mean (SEM), and means indicated by black squares.

To explore the relationship between reading variables and catch-up saccades (CS) per second, a Principal Component Analysis (PCA) was applied to a set of oculomotor features using the `**pca**` function in MATLAB. These features included the mean amplitude of progressive and regressive saccades, mean fixation duration, microsaccades per second, saccades per second, progressions per second, regressions per saccade, spatial and temporal entropy, and reading duration. The primary objective of performing PCA was to reduce the dimensionality of the data and to identify key patterns among these variables that could explain variability in catch-up saccades[34,35]. Following the PCA, the first three principal components (PC1, PC2, and PC3) were selected based on their contribution (77.59%) to the overall variance. These components were subsequently used as predictors in a linear regression model, where the mean catch-up saccades per second served as the outcome variable. This regression model was used to examine how the different principal components, which represent various combinations of the original features, could predict the rate of catch-up saccades. The linear regression model included an intercept and the three principal components as predictors. The performance of the model was evaluated using the R-squared and adjusted R-squared values, which describe the proportion of variance in the dependent variable explained by the independent variables. Additionally, the RMSE was used to assess the average prediction error, and the F-statistic provided a test of the overall model significance. The analysis was performed on 395 observations, with 391 degrees of freedom remaining for the error term.

Finally, a correlation analysis was performed to examine the relationship between smooth pursuit and reading parameters, specifically focusing on the microsaccades rate during reading and PUR catch-up saccades per second, as well as the reading microsaccades' spatial entropy and PUR saccades' spatial entropy.

Results

The aim of the study was to investigate the relationship between eye movement patterns during reading and during the tracking of a moving object in a cohort of adults, displaying various reading speeds, yet without inclusion of subjects diagnosed with dyslexia. This study utilized a dataset comprising 407 native English-speaking college students[30]. After excluding 12 subjects due to significant data artifacts and missing key variables from the original dataset, the final dataset included 395 subjects. Participants completed the tasks up to six times over three recording rounds, providing a longitudinal dataset. In what follows we first describe the effects for each task individually, before considering eye movement correlations across task conditions.

Adaptive microsaccade control limits reading speed

The reading task involved presenting text excerpts to participants, with different excerpts used across various sessions and rounds. Data preprocessing included imputing missing values and normalizing the 'Duration' metric using Z-scores. The analysis focused on metrics such as mean fixation duration, microsaccades per second, spatial and temporal entropy, ratio of regressive saccades to total saccades, mean amplitude of regressive and progressive saccades, and progressive saccades per second (Table 1 shows the descriptive statistics of these parameters).

Significant positive correlations were found between reading duration and mean fixation duration, ratio of regressive saccades to total saccades, microsaccades per second, spatial entropy, and temporal entropy. This indicates that longer reading durations are associated with longer fixation times, more frequent regressive saccades, a higher rate of microsaccades, and greater spatial and temporal variability in eye movements. Conversely, negative correlations were observed between reading duration and the mean amplitude of progressive saccades, suggesting that longer reading durations are associated with smaller progressive saccades (summary of results in Table 2). These findings are consistent with prior research[2,4,36–41].

While the correlation analysis provides valuable insights into the linear relationships between variables, it does not capture the potential nonlinear dependencies that might exist among the reading parameters. Therefore, a GAM was employed to further investigate these relationships, providing insights into both linear and nonlinear dependencies.

Variable	Mean ($n=395$)	SD
Duration (s)	53.26	13.74
Mean fixation duration (ms)	284.33	38.20
Microsaccades per second (s^{-1})	0.45	0.26
Spatial entropy	1.21	0.05
Temporal entropy	3.57	1.04
Ratio of regressive saccades	0.25	0.06
Mean amplitude of regressive saccades (deg)	3.81	0.74
Progressive saccades per Second (Sac/s)	2.47	0.35
Mean amplitude of progressive Saccades (deg)	5.52	0.76

Table 1. Descriptive statistics of reading parameters.

Variable	Correlation Coefficient	*p*-value	95% CI (Lower)	95% CI (Upper)
Mean fixation duration	0.47	4.66e-23	0.39	0.54
Microsaccades per second	0.20	5e-05	0.11	0.30
Spatial entropy	0.44	8.13e-20	0.35	0.51
Temporal entropy	0.43	2.03e-19	0.35	0.51
Ratio of regressive saccades	0.21	1.86e-05	0.12	0.31
Mean amplitude of regressive saccades	−0.18	0.000358	−0.27	−0.08
Progressive saccades per second	−0.42	1.35e-18	−0.50	−0.34
Mean amplitude of progressive saccades	−0.50	2.23e-26	−0.57	−0.42

Table 2. Analysis results of correlation with reading duration.

Approximate significance of smooth terms	edf	Ref.df	F	*p*-value
Microsaccades per second	6.779	7.870	14.239	< 2e-16 ***
Spatial entropy	4.160	5.105	6.562	6.85e-06 ***
Temporal entropy	4.056	5.119	31.518	< 2e-16 ***
Mean amplitude of regressive saccades	3.991	4.978	11.915	< 2e-16 ***
Progressive saccades per second	1.976	2.543	41.205	< 2e-16 ***

Table 3. GAM Model summary.

The GAM included smooth terms for microsaccades per second, spatial entropy, temporal entropy, mean amplitude of regressive saccades, and progressive saccades per second, allowing for modeling of intricate nonlinear dependencies. A linear term was applied to the mean amplitude of progressive saccades.

The GAM analysis revealed significant effects for several variables. For the parametric coefficients, the mean amplitude of progressive saccades (Estimate = −0. 0.27707, Std. Error = 0.03712, t = −7.463, $p = 6.23e-13$) was a significant predictor of reading duration. The results for the smooth terms of the GAM are summarized in Table 3. These results provide additional confirmation of the correlation findings and highlight the importance of these metrics in understanding reading behavior.

Significant positive correlations between reading duration and both spatial and temporal entropy suggest that more complex eye movement patterns are associated with longer reading times. The GAM model highlights the intricate nonlinear dependencies between these parameters, with higher rates of microsaccades, greater spatial dispersion, and more varied temporal patterns correlating with longer reading durations.

The RMSE of 0.51, which is lower than the standard deviation of the dependent variable (0.9959), indicates relatively good model accuracy, suggesting that the GAM model provides a robust framework for predicting reading duration based on the analyzed parameters. The model's effectiveness is further demonstrated by the adjusted R-squared value of 0.719. Additionally, the deviance explained was 75.8%, with a Generalized Cross-Validation (GCV) score of 0.295 and a scale estimate of 0.278, underscoring the model's ability to capture the variability in reading duration.

To study these findings in greater detail, a t-test was performed to compare individuals with a reading duration 2 standard deviations higher than the mean (slow readers) to the rest of the study sample. Results showed significant increases in their rates of microsaccades, spatial entropy, and temporal entropy. Specifically, the microsaccade rate for these individuals was 0.54 standard deviations above the overall mean microsaccade rate ($p = 0.034$, 95% CI = [0.04, 1.04]). Their spatial entropy was 1.28 standard deviations higher than the overall mean spatial entropy ($p = 0.010$, 95% CI = [0.34, 2.23]), and their temporal entropy was 1.20 standard deviations above the overall mean temporal entropy ($p = 2.246559e-05$, 95% CI = [0.73, 1.60]).

These findings indicate that slow readers exhibit significantly higher rates of microsaccades, spatial entropy, and temporal entropy of microsaccades than the rest of the study sample, reinforcing the importance of these metrics in reading behavior analysis (Fig. 2).

Speed and direction of the moving stimuli affect tracking efficiency during smooth pursuit

In order to investigate eye movement patterns and foveation strategies outside the reading range, we performed similar analyses during an object tracking (PUR) task. In the PUR task, participants followed a horizontally moving black sphere at speeds of 5, 10, and 20 dva/s. The sphere moved smoothly between the left and right edges of the viewing region, pausing at the edges. The analysis focused on the rate of catch-up saccades, position error, and velocity error. The statistical analysis reveals significant effects of speed and direction on Position Error (PE), Velocity Error (VE), and catch-up saccades per second, with notable interaction effects indicating that the impact of speed varies by direction. For velocity error (Fig. 3a), the ANOVA results indicated a significant effect of speed ($F = 622.45$, $p = 0.0016$) with larger errors at 20 dva/s compared to 5 and 10 dva/s, although no significant effect of direction ($F = 0.22$, $p = 0.68$) or interaction between speed and direction ($F = 1.2$, $p = 0.3$) was observed. Analysis of position error (Fig. 3b) revealed notable speed-related variations ($F = 26.54$, $p = 0.0363$), indicating an increase in position errors with increasing target speed. Particularly, when the stimulus moved leftward, errors intensified

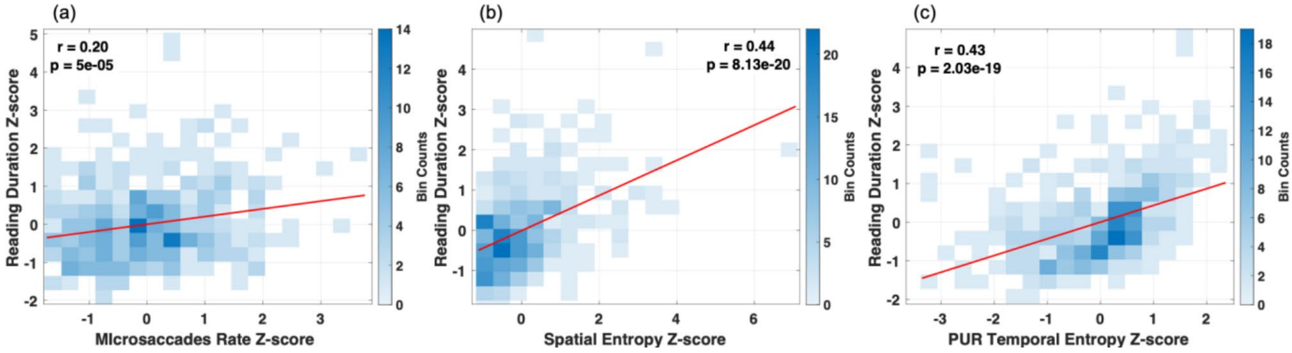

Fig. 2. Relationship between reading duration and eye movement metrics for all subjects. Each subplot depicts the correlation with: **(a)** microsaccades rate, **(b)** spatial entropy, and **(c)** temporal entropy.

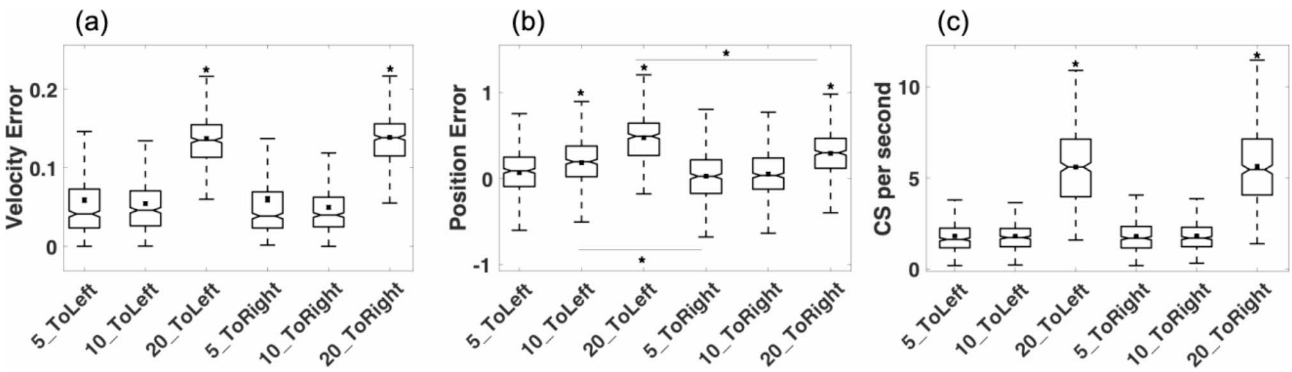

Fig. 3. Effect of object speed and direction on eye movement parameters (**a**) velocity error, (**b**) position error, and (**c**) catch-up saccades (CS) per second during PUR task performance.

across all speeds, while towards the right, errors were notably heightened at 20 dva/s compared to slower speeds. Moreover, the interaction between speed and direction uncovered significant discrepancies (F = 7.3, $p = 0.0007$), with notably higher errors observed towards the left compared to the right at speeds of 10 and 20 dva/s.

Moreover, the catch-up saccades rate (CS per second) (Fig. 3c) was significantly influenced by speed (F = 1948.68, $p = 0$), with an increase in their occurrence as speed increased. However, neither direction (F = 0.24, $p = 0.62$) nor the interaction between speed and direction (F = 0.39, $p = 0.67$) had a significant influence.

Microsaccadic and saccadic activity during reading as Key predictors of catch-up saccades rate during PUR: insights from PCA and regression

The relationship between smooth pursuit eye movements and key indicators of reading performance is explored using PCA and regression models to uncover shared oculomotor mechanisms influencing performance across both tasks. PCA was performed on the Z-score-transformed values of nine reading-related features: mean amplitude of progressive saccades, mean amplitude of regressive saccades, mean fixation duration, microsaccades per second, progressions per second, ratio of regressive saccades to total saccades, spatial entropy of microsaccades, temporal entropy of microsaccades, and reading duration. The first three principal components (PC1, PC2, and PC3) were selected for further analysis based on their contributions to the total variance in the data.

PC1 was primarily driven by microsaccades per second, spatial entropy of microsaccades, temporal entropy of microsaccades, and reading duration, which all showed positive loadings (0.40, 0.43, 0.49, and 0.40, respectively). These strong positive loadings suggest that PC1 captures variability related to microsaccadic activity, their spatial and temporal entropy, and reading duration. In the linear regression model, PC1 was a significant predictor of mean catch-up saccades per second, with an estimated coefficient of 0.2031 (SE = 0.0237, t = 8.57, $p < 0.0001$). This positive association indicates that an increase in PC1 is linked to an increase in the rate of catch-up saccades, implying that participants with higher microsaccadic activity and greater spatial and temporal entropy of microsaccades in their reading patterns tend to exhibit more catch-up saccades.

PC2 is characterized by a strong positive loading for progressions per second (0.54) and a negative loading for mean fixation duration (−0.34). However, despite this high saccadic activity, reading duration (loading = −0.03) is not impacted. This is because the pattern also includes short fixation durations and a low rate of regressive saccades (loading = −0.40), which together allow for rapid progression through the text without the need for additional reading time. In the regression model, PC2 was a significant predictor of catch-up saccades during

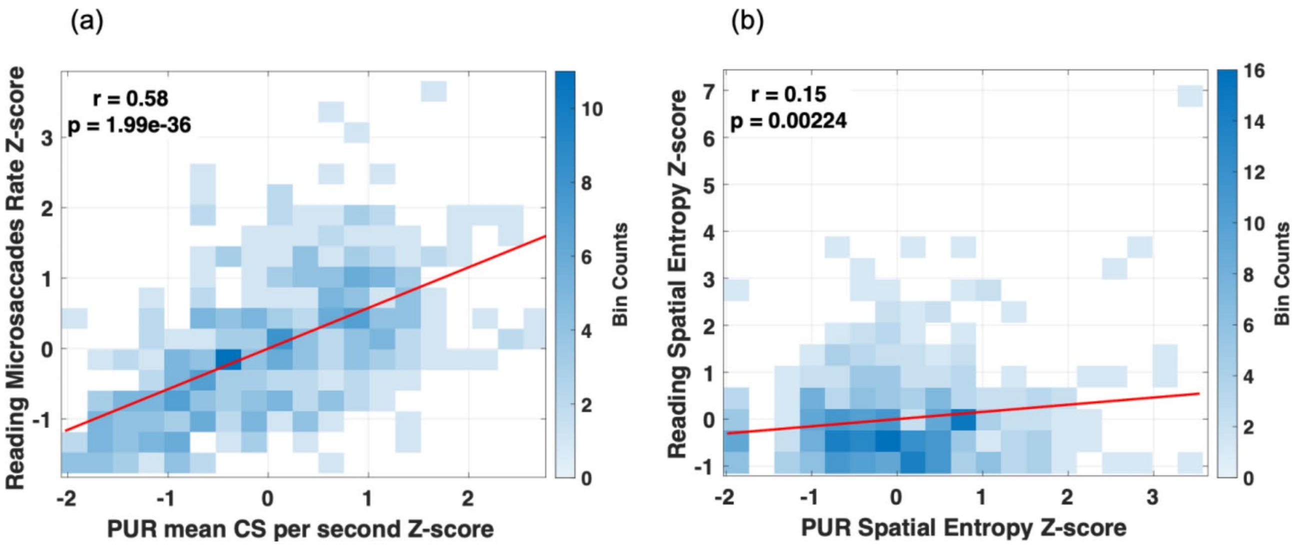

Fig. 4. Relationship between reading and PUR task performance (**a**) Correlation between the mean catch-up saccades per second during PUR and microsaccades rate during reading, (**b**) correlation between spatial entropies during reading and smooth pursuit.

the smooth pursuit task, with a positive coefficient of 0.1984 (SE = 0.0294, t = 6.76, $p < 0.0001$). This association suggests that individuals displaying this reading pattern—marked by frequent, brief forward saccades—also tend to exhibit more catch-up saccades during smooth pursuit. However, in reading, the combination of short fixation durations and fewer regressions balances out the high saccadic rate, preventing an increase in overall reading duration.

PC3 is characterized by a high loading for mean fixation duration (0.5566) and a moderate loading for reading duration (0.3827), suggesting that this component reflects a reading pattern with prolonged fixations and extended reading time. This pattern is associated with low saccadic activity, as indicated by the negative loadings for microsaccades per second (−0.3396) and regressions on saccades (−0.3438). The lower rate of regressive saccades suggests that readers with high PC3 scores engage in fewer corrective movements, possibly due to a more deliberate, slower reading style that emphasizes steady fixation on each word or line. In the regression model, PC3 was a significant predictor of catch-up saccades during smooth pursuit, with a negative coefficient of −0.2214 (SE = 0.0326, t = −6.78, $p < 0.0001$). This negative association indicates that individuals with higher PC3 scores (i.e., those with longer fixations and lower saccadic activity) tend to have fewer catch-up saccades in smooth pursuit. This relationship suggests that a reading style marked by extended fixations and minimal regressions and microsaccades per second aligns with more stable tracking behavior during smooth pursuit, thus reducing the need for corrective saccades. The overall regression model explained 29.7% of the variance in catch-up saccades per second, with an R-squared of 0.297 and an adjusted R-squared of 0.292, indicating a moderate explanatory power. The Root Mean Squared Error (RMSE) was 0.842, suggesting a moderate level of prediction error. The model's significance was supported by an F-statistic of 55 ($p < 0.0001$), demonstrating a substantial improvement over the constant-only model.

Significant predictive relationship between smooth pursuit eye movements and reading performance indicators

To further investigate the relationship between smooth pursuit performance and reading capabilities, we examined the correlation between the catch-up saccades per second during smooth pursuit object tracking and microsaccades rate during reading. Additionally, we explored the correlation between the spatial entropy of microsaccades during reading and the spatial entropy of catch-up saccades during smooth pursuit. Catch-up saccades were selected as a performance indicator for smooth pursuit due to their pronounced sensitivity to speed variations, as evidenced by a significant F-value of 1948.68 from ANOVA testing. Moreover, this choice is based on the premise that both microsaccades and catch-up saccades reflect underlying oculomotor control mechanisms, and PCA results revealed significant relationships between these oculomotor variables. Therefore, analyzing their relationship may provide insights into common neural processes involved in both reading and smooth pursuit tasks.

The analysis included data across various experimental conditions, encompassing speeds of 5, 10, and 20 dva/s and both leftward and rightward directions. This data was aggregated into a single measure, mean catch-up saccades per second, to streamline the analysis.

The correlation analysis yielded robust results across the different relationships tested (Fig. 4). The correlation between mean catch-up saccades per second and microsaccades rate was moderate, with a Pearson correlation coefficient of $r = 0.58$, a 95% confidence interval of [0.51, 0.64], and a highly significant p-value ($p = 1.99e-36$). This result underscores a significant statistical linkage between these two variables.

The spatial entropy of reading microsaccades and the spatial entropy of smooth pursuit catch-up saccades showed a weak positive correlation, with a Pearson correlation coefficient of $r = 0.15$, a 95% confidence interval of [0.06, 0.25], and a significant p-value ($p = 0.00224$).

Discussion

This research investigates the impact of oculomotor dynamics on both reading and non-verbal visual tasks, such as smooth pursuit. This approach broadens our understanding of the common oculomotor control mechanisms that govern these distinct yet related tasks. We investigated foveation efficiency during reading and smooth pursuit in a cohort of 395 subjects from a public database of eye movement behavior collected with a virtual reality (VR) headset. The results confirm our initial hypothesis that slow readers display poor foveation not only during reading but also during smooth pursuit. In the following sections, we first discuss limitations of the VR based approach, how our findings link to previous literature, before concluding with thoughts on the possible role of omnipause neurons in adequate reading function.

A limitation of our study to keep in mind is its reliance on virtual reality. In this VR-based environment, each letter subtended approximately 1 dva, a size notably larger than the letter sizes typically used in standard screen-based reading, as seen in studies such as[42,43]. This larger letter size likely influenced observed saccade amplitudes and fixation behaviors. Specifically, the mean progressive saccade amplitude in our study was around 5.52 degrees, translating to approximately 5–6 letters per saccade. This character span aligns with findings from traditional setups, where mean saccade amplitudes in adults range from approximately 6 to 8 characters[42–45].

Another limitation of the VR environment in this study is the utilization of an eye tracker, which operates at a sampling rate of 250 Hz and provides a spatial accuracy of 0.2 dva. Although this sampling rate is on the lower end of what is typically used for high-precision eye-tracking research, it has been validated in a previous study investigating microsaccades[7]. The fixation durations we measured were somewhat elevated compared to those observed in non-VR studies. While our study found an average fixation duration of 284 ms, traditional studies report shorter times in adults, such as 240 ms[45], 235 ms[43], and 205 ms[44]. Though VR reading studies are limited, Mirault et al. (2021) reported mean first fixation durations were around 380 ms for words and 450 ms for pseudowords in children within a similar environment[46]. Notably, longer fixation durations have also been observed in non-VR contexts, with Huestegge et al. (2009) reporting mean durations of 358 ms in children and 297 ms in adults[42]. In our case, the increased fixation durations may stem from the immersive setting, which can impact visual processing and reading strategies due to altered perceptual cues or heightened cognitive load.

Our results show that slow readers have a higher rate of microsaccades and greater spatial and temporal entropy of microsaccades during reading. These findings distinguish slow and fast readers based on reading duration, as comprehension assessments were not included in the original dataset. Nonetheless, these findings are consistent with Bowers and Poletti[4], who demonstrated that slow readers exhibit a higher rate of microsaccades. Similarly, Rima and Schmid[2]found that slow readers, whether diagnosed with developmental dyslexia or neurotypical, display a higher rate of microsaccades and greater spatial and temporal unpredictability during reading, though not during free viewing. Additionally, we observed that slow readers with increased microsaccade rates also exhibited progressive saccades with smaller amplitudes and more regressive saccades, aligning with previous studies[36–41].

Furthermore, we found that foveation limitations in slow readers also manifested during smooth pursuit as increased rate of catch-up saccades. The PCA results indicate that key oculomotor metrics, such as saccadic and microsaccadic activity, contribute to variability across both reading and pursuit tasks. Our study specifically reveals that the increased spatial entropy and rate of microsaccades during reading are correlated with increased spatial entropy and rate of catch-up saccades during smooth pursuits. This overlap suggests shared mechanisms of oculomotor control across these tasks, supporting the relevance of these metrics in both contexts. Related findings by Black, Collins et al.[27] and Yang, Vernet et al.[47] enhance our understanding by illustrating how variations in smooth pursuit characteristics and saccadic components can signal underlying reading difficulties. For instance, Black et al. reported that a significant portion of poor readers displayed unusual saccadic behaviors during pursuit, while Yang et al. observed that dyslexic children exhibit higher disconjugacy during rightward pursuits. Despite analyzing data from a large cohort, we lacked explicit information on dyslexia diagnoses, suggesting that further investigation among dyslexic individuals could provide valuable insights into reading patterns and performance outcomes.

What might be the neuronal origin of these foveation limitations observed both during reading and during smooth pursuit? Saccadic eye movement generation and thus foveation stability are modulated by a push/pull relationship between neurons in the superior colliculus and omnipause neurons, situated in the nucleus raphe interpositus of the paramedian pontine reticular formation. These neurons maintain a sustained firing rate during fixation and cease firing during saccades, irrespective of the size or direction of the saccades. This effectively inhibits the generation of saccades by suppressing the activity of saccade-related premotor burst neurons located in the mesencephalic and pontomedullary reticular formations[48,49]. Following stimulus onset, their activity increases, aiding in the adaptation and processing of new visual information, thereby maintaining focused and efficient visual perception[50,51]. These neurons play a pivotal role in regulating eye movements, ensuring efficient smooth pursuit, and inhibiting inappropriate saccades during fixation[52]. During microsaccades, omnipause neurons in the brainstem exhibit pauses similar to those observed during larger saccades, albeit of shorter duration[53–55]. Additionally, the population of saccade-related burst neurons in the brainstem, active during larger saccades, also demonstrate bursts during microsaccades[54,56]. Moreover, they adhere to a similar main sequence curve[57], suggesting a common motor control mechanism governs the generation of both types of eye movements. The study "Common Inhibitory Mechanism for Saccades and Smooth-Pursuit Eye Movements" by M. Missal and E. L. Keller reveals that omnipause neurons, previously thought to only inhibit saccades, also significantly reduce activity during smooth pursuit eye movements[51]. This suggests a shared inhibitory mechanism for both types of eye movements (for reviews, see Krauzlis, 2004[58]; Orban de Xivry and Lefevre, 2007[18]; Goettker and Gegenfurtner, 2021[59]). During saccades, OPNs completely stop firing, acting as a gate, while during smooth pursuit, their activity decreases but does not stop, correlating with eye velocity and pursuit duration. This modulatory function of the OPN allows the system to adapt to varying oculomotor needs and challenges. We suggest that slow readers with elevated rates of microsaccades and catch-up saccades may experience varying levels of modulation activity from omnipause neurons. Poor modulatory activity would lead to inopportune eye movements during foveation, negatively affecting both reading performance and smooth pursuit efficiency. Further research into omnipause neuron activity is necessary to clarify their specific role in oculomotor control and reading fluency.

In conclusion, this study leveraged a substantial dataset to corroborate the association between elevated microsaccade rates, increased spatial and temporal entropy, and lower reading fluency, aligning with previous findings from smaller sample sizes. These oculomotor anomalies were also evident during smooth pursuit tasks, reflected in the increased rates of catch-up saccades and their spatial unpredictability. These results underscore the shared oculomotor control mechanisms underlying reading and non-verbal visual tasks. Future research should further explore the role of omnipause neurons in reading processes. Additionally, studies should examine the oculomotor behaviors in dyslexic individuals and young children to enhance early detection and intervention strategies for reading difficulties.

Data availability

The final processed data are available as supplementary files in 'ProcessedData.zip'. This archive includes 'ALL.csv' for various parameters of smooth pursuit and reading for each subject, 'CSpersecond.csv' for the mean catch-up saccades per second per direction and speed, 'PositionError.csv' for the mean position error per condition, and 'VelocityError.csv' for the mean velocity error per condition. All the figures are generated using MATLAB Version 9.13 (R2022b).

Received: 29 July 2024; Accepted: 13 December 2024
Published online: 24 February 2025

References

1. Clark, A. M. et al. Eye drift during fixation predicts visual acuity. *Proc. Natl. Acad. Sci.* **119** (49), e2200256119 (2022).
2. Rima, S. & Schmid, M. C. Reading specific small saccades predict individual phonemic awareness and reading speed. *Front. NeuroSci.* **15**, 663242 (2021).
3. Loughnane, G. M. et al. Antagonistic interactions between microsaccades and evidence accumulation processes during decision formation. *J. Neurosci.* **38** (9), 2163–2176 (2018).
4. Bowers, N. R. & Poletti, M. Microsaccades during reading. *PloS one*. **12** (9), e0185180 (2017).
5. Alexander, R. G. & Martinez-Conde, S. *Fixational eye movements*, in *Eye movement research: An introduction to its scientific foundations and applications*. pp. 73–115. (2019).
6. Engbert, R. Microsaccades: A microcosm for research on oculomotor control, attention, and visual perception. *Prog. Brain Res.* **154**, 177–192 (2006).
7. Engbert, R. & Kliegl, R. Microsaccades uncover the orientation of covert attention. *Vision. Res.* **43** (9), 1035–1045 (2003).
8. Cornsweet, T. N. Determination of the stimuli for involuntary drifts and saccadic eye movements. *JOSA* **46** (11), 987–993 (1956).
9. Hauperich, A. K., Young, L. K. & Smithson, H. E. *What makes a microsaccade? A review of 70 years of research prompts a new detection method. J. Eye Mov. Res.*, **12**(6). (2019).
10. Rolfs, M., Kliegl, R. & Engbert, R. Toward a model of microsaccade generation: The case of microsaccadic inhibition. *J. Vis.* **8** (11), 5–5 (2008).
11. Bergeron, A. & Guitton, D. multiple-step gaze shifts: omnipause (OPNs) and collicular fixation neurons encode gaze position error; OPNs gate saccades. *J. Neurophysiol.* **88** (4), 1726–1742 (2002).
12. Krauzlis, R. J., Goffart, L. & Hafed, Z. M. Neuronal control of fixation and fixational eye movements. *Philosophical Trans. Royal Soc. B: Biol. Sci.* **372** (1718), 20160205 (2017).
13. Festa, D. et al. Neuronal variability reflects probabilistic inference tuned to natural image statistics. *Nat. Commun.* **12** (1), 3635 (2021).
14. Veldre, A. & Andrews, S. Lexical quality and eye movements: Individual differences in the perceptual span of skilled adult readers. *Q. J. Experimental Psychol.* **67** (4), 703–727 (2014).
15. Yablonski, M. et al. Microsaccades are sensitive to word structure: A novel approach to study language processing. *Sci. Rep.* **7** (1), 3999 (2017).
16. Hafed, Z. M. & Krauzlis, R. J. Microsaccadic suppression of visual bursts in the primate superior colliculus. *J. Neurosci.* **30** (28), 9542–9547 (2010).
17. Rolfs, M. & Ohl, S. Visual suppression in the superior colliculus around the time of microsaccades. *J. Neurophysiol.* **105** (1), 1–3 (2011).
18. Orban de Xivry, J. J. & Lefevre, P. Saccades and pursuit: two outcomes of a single sensorimotor process. *J. Physiol.* **584** (1), 11–23 (2007).
19. Spering, M. & Montagnini, A. Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review. *Vision. Res.* **51** (8), 836–852 (2011).
20. Luebke, A. & Robinson, D. Transition dynamics between pursuit and fixation suggest different systems. *Vision. Res.* **28** (8), 941–946 (1988).
21. Robinson, D. The systems approach to the oculomotor system. *Vision. Res.* **26** (1), 91–99 (1986).
22. Carl, J. & Gellman, R. Human smooth pursuit: stimulus-dependent responses. *J. Neurophysiol.* **57** (5), 1446–1463 (1987).
23. De Brouwer, S. et al. What triggers catch-up saccades during visual tracking? *J. Neurophysiol.* **87** (3), 1646–1650 (2002).
24. Boman, D. K. & Hotson, J. R. Predictive smooth pursuit eye movements near abrupt changes in motion direction. *Vision. Res.* **32** (4), 675–689 (1992).
25. Bahill, A. T. & McDonald, J. D. Smooth pursuit eye movements in response to predictable target motions. *Vision. Res.* **23** (12), 1573–1583 (1983).
26. Churchland, A. K. & Lisberger, S. G. Gain control in human smooth-pursuit eye movements. *J. Neurophysiol.* **87** (6), 2936–2945 (2002).
27. Black, J. et al. Smooth pursuit eye movements in normal and dyslexic children. *Percept. Mot. Skills*. **59** (1), 91–100 (1984).

28. Callu, D. et al. Smooth pursuit eye movements are associated with phonological awareness in preschool children. *Brain Cogn.* **58** (2), 217–225 (2005).
29. Judge, J., Caravolas, M. & Knox, P. C. Smooth pursuit eye movements and phonological processing in adults with dyslexia. *Cognit. Neuropsychol.* **23** (8), 1174–1189 (2006).
30. Lohr, D. et al. *GazeBaseVR, a large-scale, longitudinal, binocular eye-tracking dataset collected in virtual reality*. *Sci. Data*, **10**(1). (2023).
31. Shannon, C. E. A mathematical theory of communication. *Bell Syst. Tech. J.* **27** (3), 379–423 (1948).
32. Wood, S. N. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J. Am. Stat. Assoc.* **99** (467), 673–686 (2004).
33. Niehorster, D. C. et al. Characterizing gaze position signals and synthesizing noise during fixations in eye-tracking data. *Behav. Res. Methods.* **52**, 2515–2534 (2020).
34. Raiko, T., Ilin, A. & Karhunen, J. *Principal component analysis for sparse high-dimensional data*. in *International Conference on Neural Information Processing*. Springer. (2007).
35. Jolliffe, I. T. & Cadima, J. *Principal component analysis: a review and recent developments.* Philosophical transactions of the royal society A: Mathematical, Physical and Engineering Sciences, 374(2065): p. 20150202. (2016).
36. Eden, G. et al. Differences in eye movements and reading problems in dyslexic and normal children. *Vision. Res.* **34** (10), 1345–1358 (1994).
37. Biscaldi, M., Gezeck, S. & Stuhr, V. Poor saccadic control correlates with dyslexia. *Neuropsychologia* **36** (11), 1189–1202 (1998).
38. Prado, C., Dubois, M. & Valdois, S. The eye movements of dyslexic children during reading and visual search: impact of the visual attention span. *Vision. Res.* **47** (19), 2521–2530 (2007).
39. Trauzettel-Klosinski, S. et al. Eye movements in German-speaking children with and without dyslexia when reading aloud. *Acta Ophthalmol.* **88** (6), 681–691 (2010).
40. Hatzidaki, A. et al. Reading and visual processing in Greek dyslexic children: an eye-movement study. *Dyslexia* **17** (1), 85–104 (2011).
41. Bellocchi, S. et al. I can read it in your eyes: What eye movements tell us about visuo-attentional processes in developmental dyslexia. *Res. Dev. Disabil.* **34** (1), 452–460 (2013).
42. Huestegge, L. et al. Oculomotor and linguistic determinants of reading development: A longitudinal study. *Vision. Res.* **49** (24), 2948–2959 (2009).
43. Rayner, K. Eye movements and the perceptual span in beginning and skilled readers. *J. Exp. Child Psychol.* **41** (2), 211–236 (1986).
44. Häikiö, T. et al. Development of the letter identity span in reading: Evidence from the eye movement moving window paradigm. *J. Exp. Child Psychol.* **102** (2), 167–181 (2009).
45. Blythe, H. I. et al. The binocular coordination of eye movements during reading in children and adults. *Vision. Res.* **46** (22), 3898–3908 (2006).
46. Mirault, J. et al. Using virtual reality to assess reading fluency in children. in Frontiers in Education. Frontiers Media SA. (2021).
47. Yang, Q. et al. *Binocular coordination during smooth pursuit in dyslexia: a multiple case study*. *J. Eye Mov. Res.*, **3**(3). (2010).
48. Moschovakis, A. K., Scudder, C. A. & Highstein, S. M. The microscopic anatomy and physiology of the mammalian saccadic system. *Prog. Neurobiol.* **50** (2–3), 133–254 (1996).
49. Scudder, C. A., Kaneko, C. R. & Fuchs, A. F. The brainstem burst generator for saccadic eye movements: a modern synthesis. *Exp. Brain Res.* **142**, 439–462 (2002).
50. Everling, S. et al. Comparison of the discharge characteristics of brain stem omnipause neurons and superior colliculus fixation neurons in monkey: implications for control of fixation and saccade behavior. *J. Neurophysiol.* **79** (2), 511–528 (1998).
51. Missal, M. & Keller, E. Common inhibitory mechanism for saccades and smooth-pursuit eye movements. *J. Neurophysiol.* **88** (4), 1880–1892 (2002).
52. Lemos, J. & Eggenberger, E. Saccadic intrusions: review and update. *Curr. Opin. Neurol.* **26** (1), 59–66 (2013).
53. Keller, E. Participation of medial pontine reticular formation in eye movement generation in monkey. *J. Neurophysiol.* **37** (2), 316–332 (1974).
54. Van Gisbergen, J., Robinson, D. A. & Gielen, S. A quantitative analysis of generation of saccadic eye movements by burst neurons. *J. Neurophysiol.* **45** (3), 417–442 (1981).
55. Brien, D. C. et al. *The behavioural and neurophysiological modulation of microsaccades in monkeys*. *J. Eye Mov. Res.*, **3**(2). (2010).
56. Van Horn, M. R. & Cullen, K. E. Coding of microsaccades in three-dimensional space by premotor saccadic neurons. *J. Neurosci.* **32** (6), 1974–1980 (2012).
57. Zuber, B. L., Stark, L. & Cook, G. Microsaccades and the velocity-amplitude relationship for saccadic eye movements. *Science* **150** (3702), 1459–1460 (1965).
58. Krauzlis, R. J. Recasting the smooth pursuit eye movement system. *J. Neurophysiol.* **91** (2), 591–603 (2004).
59. Goettker, A. & Gegenfurtner, K. R. A change in perspective: The interaction of saccadic and pursuit eye movements in oculomotor control and perception. *Vision. Res.* **188**, 283–296 (2021).

Acknowledgements

We thank Lohr, Aziz et al. for their work in assembling the dataset that formed the basis for this analysis. Their efforts in collecting and sharing these data have made this study possible. We also thank Walid Mawass for his enriching discussions about avenues for statistical analysis. This work is supported by a Swiss Government Excellence Scholarship to N.C. and SNSF grants 31NE30_203974 (ERA-net) and 310030_204544 to M.C.S.

Author contributions

N.C. and S.R. wrote the main manuscript text. N.C. conducted the analysis and prepared all the figures and findings. S.R. and M.C.S. developed the analytical methodology and jointly supervised the project. All authors discussed the results and implications and provided input on the manuscript throughout its development.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to M.C.S.

Reprints and permissions information is available at www.nature.com/reprints.