Individual differences in eye drift predict visual acuity

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Significance: High visual acuity is essential for humans and other species. Healthy emmetropic individuals differ considerably in their actual acuity limits. Here we show that the pattern of ocular drift during fixation also varies greatly across these observers, and that these large differences in ocular drift lead to sizable changes in the frequency content of the retinal input. We find that individual variability in acuity is accounted for by the way ocular drift reshapes visual input signals, particularly at high spatial frequencies. As a result, differences in high acuity can be predicted by differences in the characteristics of fixational drift. These findings show that besides optical and anatomical factors, ocular drift plays a critical role in modulating the limits of acuity.

Abstract: Visual acuity is essential for daily activities. It is believed that optics and anatomy alone determine the limits of visual resolution. However, in addition to these factors, eye movements greatly contribute to input dynamics, as the eyes jitter incessantly during fixation, displacing stimuli over many photoreceptors. Here we examined the relation between this motion (ocular drift) and differences in visual acuity in emmetropic observers. We show that: (a) large individual variability exists in the characteristics of ocular drifts; (b) these differences profoundly affect the structure of spatiotemporal signals to the retina; and (c) the spectral distribution of the resulting input signals strongly correlates with visual acuity. Building on these findings, we further show that individual acuity differences can be predicted from the motor behavior elicited by a simple fixation task, without directly measuring acuity. These results shed new light on how oculomotor behavior contributes to individual variability in acuity.

Introduction

High acuity is crucial for normal functioning; when vision in the central fovea is compromised, daily life activities are severely impacted[1,2]. It is therefore not surprising that visual acuity is assessed in nearly *every* eye exam. Crucially, standard assessments of acuity assume the retinal input to be approximately stationary during fixation, however, it continuously jitters as a consequence of ocular drift. Eye drift resembles a random walk, and while its small size makes it difficult to measure, on the retina it displaces the foveal image over many photoreceptors[3–5] (Fig. $1A$-B). Despite being ubiquitous, ocular drift is often ignored and it has traditionally been considered as a challenge for visual acuity as the sluggish temporal response of retinal neurons would smear spatial information as the image travels over the photoreceptors mosaic. Surprisingly, however, acuity seems to be highly resistant to this blur[6]. On the other end, the idea that fixational eye movements may instead be beneficial has a relatively long history[7] and more recent work supports this view[8–11,5,12].

Crucially, even when ocular drift is seen as beneficial, the predominant view considers high-acuity the result of a purely spatial process. However, according to an alternative proposal, fine spatial vision is the outcome of a spatiotemporal process in which ocular drift plays a critical role. Drift, in fact, introduces temporal modulations that redistribute spatial information into the temporal domain. From a receptor standpoint, larger luminance changes over time will occur at those high spatial frequencies for which drift covers a small fraction of the period. The lower the spatial frequency, the less luminance changes drift will introduce. On the other hand, for sufficiently high spatial frequencies – for which the eyes move over a larger fraction of the period – luminance changes will be attenuated. Importantly, larger luminance variations impinging on a receptor translate into higher power of the signal over a range of temporal frequencies neurons are sensitive to. As a result of this process, ocular drift selectively amplifies a range of high spatial frequencies while simultaneously attenuating the power of frequencies below and above that range[5,8,12] (Fig. $1C$). A crucial implication of this theory is that different amounts of ocular drift enhance different ranges of high spatial frequencies. Figure $1C$ demonstrates this point; smaller drifts enhance a progressively higher range of spatial frequencies.

It is known that high-acuity vision varies even across healthy emmetropes. Traditionally, optics and anatomical constraints are assumed to be the primary factors responsible for these variations[14–18]. However, previous work has also shown considerable individual differences in ocular drift[3]. It is not known to which extent these differences impact the spatiotemporal stimulus on the retina. Based on the above mentioned theory, here we speculate that the variations in ocular drift across healthy emmetropes may also play a significant role in modulating differences in visual acuity. It has already been shown that drift motion is beneficial, and absence of drift leads to reduced sensitivity[8,10,9], which is expected given that neurons in the retina and the early visual system are relatively insensitive to an unchanging input[19]. Here we examine to which extent different patterns of ocular drift influence high-acuity vision. More specifically, we predict that individuals with smaller ocular drifts have higher acuity.

Despite high-acuity vision being of paramount importance, how ocular drift interacts with the optics and anatomy

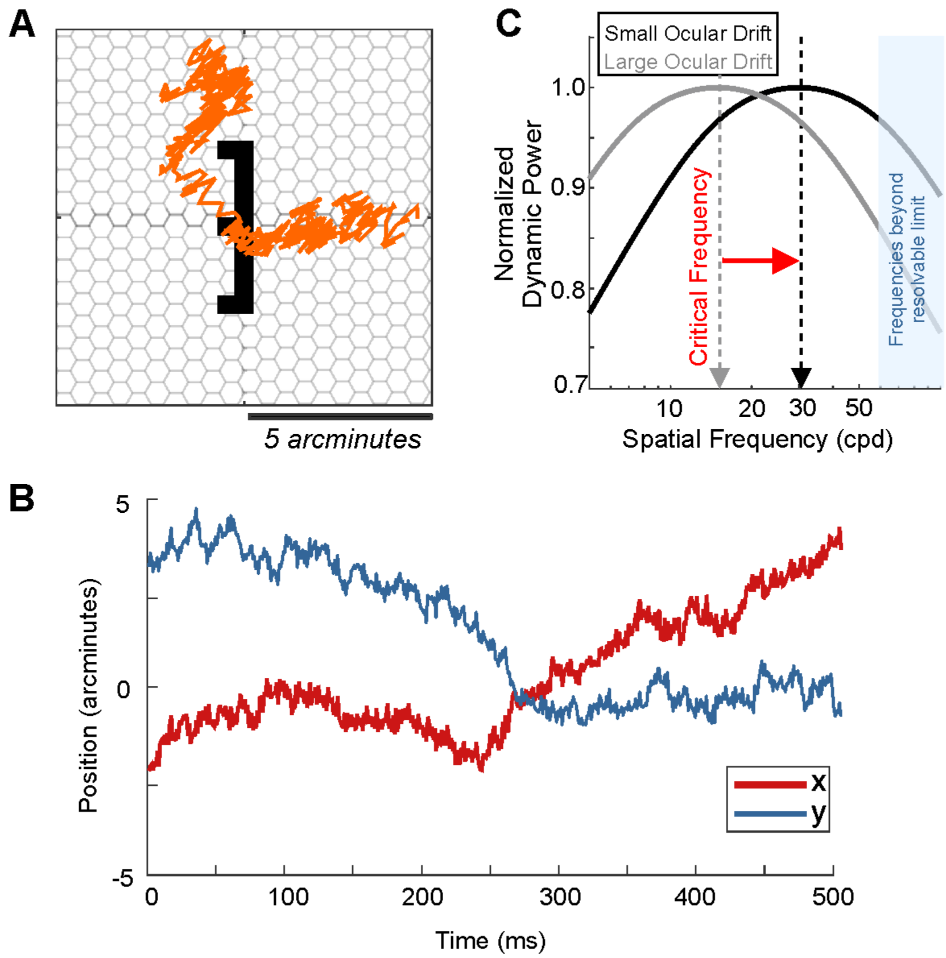

Figure 1: **Ocular Drift and its impact on the visual input.** A typical example of ocular drift from one observer while viewing one of the high-acuity stimuli used in this study (**A**-**B**). In (**A**) drift is overlaid on top of the viewed stimulus and a theoretical foveal cone photoreceptor mosaic (drawn to scale). (**B**) Drift motion on the vertical and horizontal axes as a function of time. (**C**) Amplitude of the luminance fluctuations resulting from a small and a large ocular drift at each individual spatial frequency. The power has been integrated across non-zero temporal frequencies in the sensitivity range of retinal ganglion cells. Rather than power being uniformly distributed across all the spatial frequencies, drift increases the power within a specific high spatial frequency range[12,8]. The smaller the ocular drift (black line), the higher the critical frequency (the maximally enhanced frequency). Shaded area indicates the high spatial frequencies outside of the human's visual sensitivity range[13].

of the eye to yield high-acuity vision under normal viewing conditions is still not understood. Uncovering a relationship between the amount of drift and the highest level of acuity that humans are capable of achieving will be a first crucial step to address this issue and to develop a more organic assessment of acuity, both from a scientific and clinical standpoint. Furthermore, determining if individual variations in ocular drift are associated with systematic changes in acuity will provide key evidence supporting the idea that fine spatial vision is an active process, and is heavily reliant on the temporal modulations introduced by eye motion.

Results

To determine whether individual differences in fixational drift are accompanied by differences in high-acuity vision, we measured visual acuity thresholds in healthy human observers while recording their eye movements. Fixational eye movements were recorded using a high-precision Dual Purkinje Image eye-tracker[20] coupled with a system for gaze contingent display control[21], an apparatus that enables more accurate localization of the line of sight than standard eyetracking techniques[22]. Subjects were asked to determine the identity of a briefly presented digit among four possible choices (Fig. $2A$).

We first examined the extent of ocular drift variations across healthy emmetropic subjects. Since, as shown by previous studies, eye drift can be well modeled by Brownian motion, an effective way to quantify the amount of the resulting motion in the retinal image is provided by its diffusion constant D[12]. This quantity describes how rapidly the line of sight moves away from its current location; a larger diffusion constant value reflects larger retinal motion introduced by ocular drift and it is associated to changes in drift curvature and speed. A Brownian motion model of ocular drift also enables analytical estimation of the power of the resulting luminance fluctuations. According to this model, the spatiotemporal redistribution of power resulting from ocular drift critically depends on the diffusion constant (see[12] for details). At each temporal frequency ω, power peaks at the critical spatial frequency $k_c{=}\sqrt{\omega/D}$. As a result, the power of the luminance fluctuations is largest at the critical spatial frequency, k_c (Fig. $1C$).

We found that ocular drift's diffusion constant varied greatly across individuals, changing by a factor of $\approx$4 (from 5 to 20 arcminutes^2/sec; average $\pm$ std, 13.6$'$ $\pm$ 5.0$'$) (Fig. $2B$). Similar variations in drift diffusion constant were also reported when subjects simply maintained sustained fixation on a marker (ranging from 7 to 27 arcminutes^2/sec; average $\pm$ std, 15.0$'$ $\pm$ 6.5$'$). Therefore, these findings indicate that normal ocular drift changes by a remarkably large amount from one observer to another.

Importantly, these changes in drift have a profound impact on the spatiotemporal frequency content of the input signal; smaller drifts push that range toward even higher spatial frequencies. As a result, the variations we observed in diffusion constant across subjects led to meaningful changes in the frequency content of the retinal input (Fig. $2B$). Specifically, different ranges of high spatial frequencies were enhanced across individuals. A change in diffusion constant from 5 to 20 arcminutes/sec^2 led to both a shift of approximately 15 cpd in the maximally enhanced spatial frequency (critical frequency) (Fig. 2B), and to a reduction of 64% in power in the 30-60 cpd frequency range. The critical frequency varied across subjects from 15 to 30 cpd (average $\pm$ std, 19.6 cpd $\pm$ 4.8 cpd). Based on these observations, we predicted that variations in the pattern of ocular drift across observers have an impact on their high-acuity thresholds.

Acuity thresholds also varied greatly across subjects (Fig. 2C and Supplementary Fig.1). The threshold stimulus width varied between 1.2$'$ and 1.8$'$ (1.57$'$ $\pm$ 0.21$'$) across observers; a 50% change in size between the smaller and larger measured threshold. Even though all subjects were emmetropic, acuity estimates measured during the initial screening and in the experimental task ranged between 20/20 and 20/12 on the Snellen scale, and screening and task measures were overall consistent (Supplementary Fig.2).

In line with our prediction, differences in ocular drift across subjects were strongly correlated with corresponding differences in high-acuity thresholds (p = 0.017, r = 0.728; Fig. 3A). More specifically, as one would expect from the characteristics of the luminance signal resulting from drift, the higher the acuity, the smaller the ocular drift diffusion constant. This relationship was observed both when acuity was measured psychophysically and when it was assessed with the Snellen Chart (Supplementary Fig.3). This significant relationship also holds true when measuring ocular drift's span (Supplementary Fig.4), a related measure to diffusion constant capturing primarily the spatial extent of drift motion.

We wondered whether the observed differences in drift characteristics were caused by the stimulus itself. In the experiment, the stimulus changed size following an adaptive procedure to measure acuity thresholds. Since every observer was tested extensively, the stimulus size was near threshold in the majority of the trials. This implies that, on average, subjects with worse acuity (higher thresholds) viewed larger stimuli than subjects with better acuity. Thus, a change in ocular drift with stimulus size could, in principle, also explain the observed trend. However, our data do not support this hypothesis. First, drift diffusion constant remained approximately uniform across stimulus sizes (Fig.3B, paired t-test p = 0.704, comparing diffusion constant for the smallest and the largest stimulus sizes viewed across subjects). With the exception of one subject, the difference in drift diffusion constant between the smallest and the largest stimuli tested was minimal, on average it changed of 1.8 arcminutes^2/sec $\pm$ 3.9 arcminutes^2/sec. Second, performance decreased with increasing diffusion constants even when the stimulus size was held fixed, (Fig. 3C, p = 0.024, r = -0.70). Furthermore, the same correlation between drift diffusion constant and acuity was observed when drift was measured independently from the acuity task, *i.e.* when subjects simply attempted to maintain steady fixation on a marker (p=0.029, r=0.72). Remarkably, this shows that acuity can be predicted by measuring drift diffusion constant during a simple sustained fixation task.

Importantly, as shown in Fig.4, despite individual differences in drift diffusion constant, all our subjects were well centered on the target stimuli on average. Stimuli remained within the the central 16$'$ x 16$'$ region (indicated by orange boxes in Fig.4) around the center of gaze where acuity is likely uniform[24,8], 75.7 $\pm$ 12.4% of the viewing

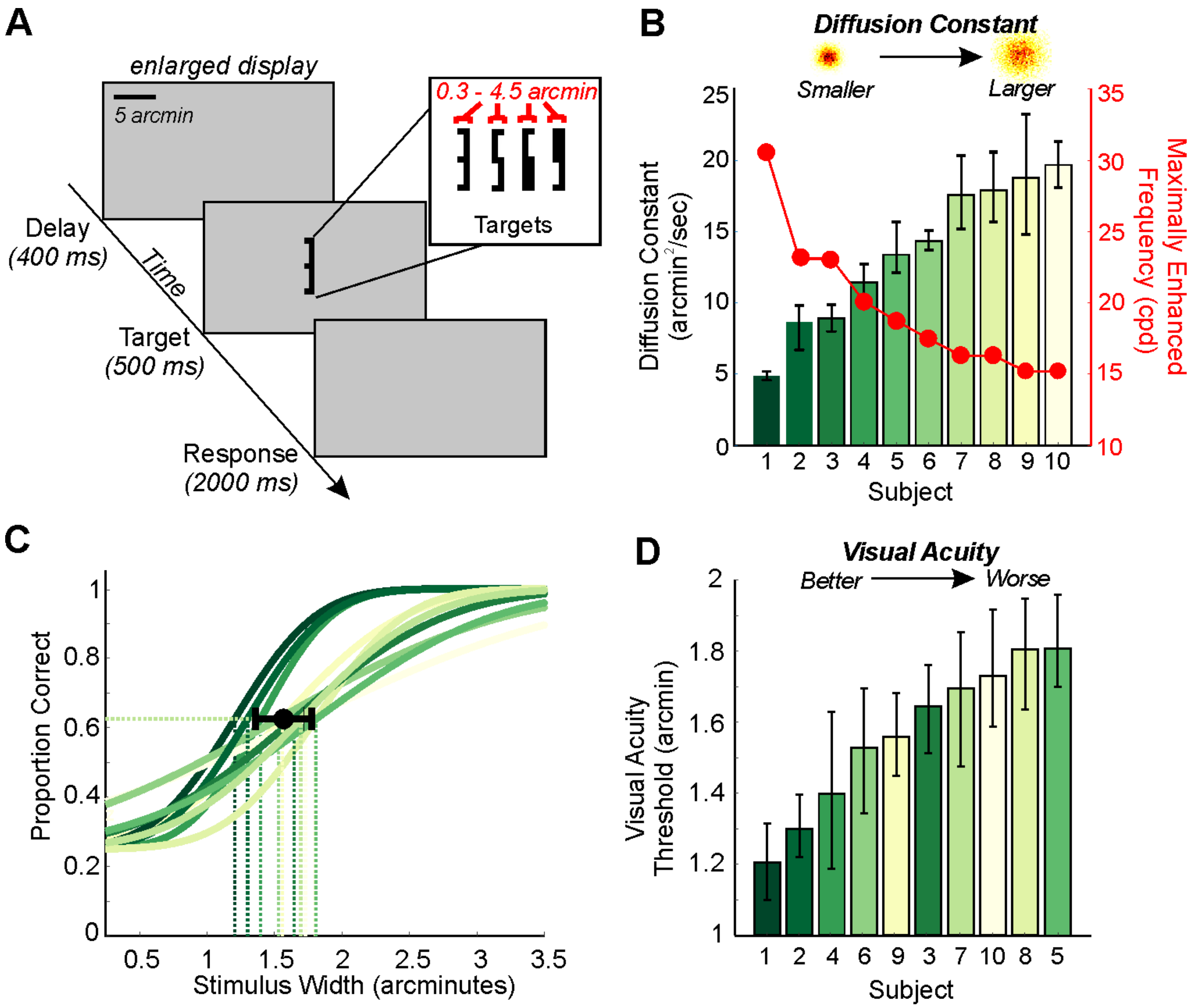

Figure 2: **Experimental procedure and behavioral results.** (**A**) Subjects were instructed to identify high-acuity stimuli presented at the center of the display for 500 ms. After a brief period of fixation, the target appeared following a delay of 400ms. Stimuli, digits in Pelli font[23], varied in size from 0.5 to 4 arcminutes. (**B**) Individual drift diffusion constants (color coded for individual subjects, with 95% bootstrapped confidence intervals), and corresponding critical frequencies (red dots). The illustrations on top represent theoretical 2D distributions of gaze position (red colors indicate higher densities) for smaller and a larger diffusion constants. (**C**) Psychometric fits and acuity thresholds (dashed lines) for single subjects (color coded as in **B** in this and following figures). Curves were fitted on ∼200 trials per subject using a cumulative Gaussian function. The average acuity threshold with ± 1 STD across subjects is also shown (black dot). (**D**) Single subject acuity. Error bars represent bootstrapped 95% confidence intervals.

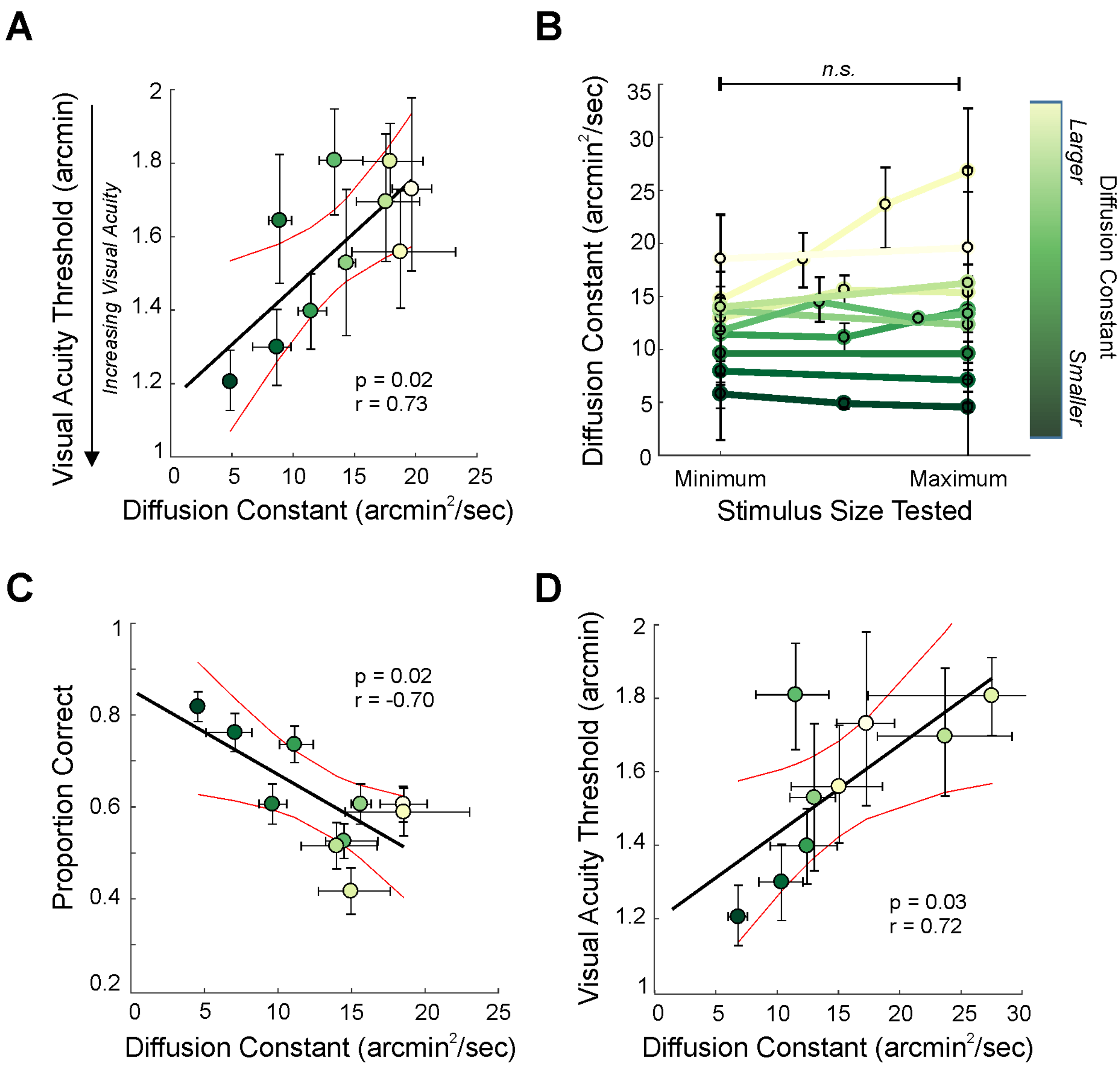

Figure 3: **Acuity thresholds and drift characteristics.** (**A**) Visual acuity thresholds as a function of diffusion constant in the task. Each point represents an individual subject, error bars are 95% confidence intervals. (**B**) Individual subject diffusion constants as a function of stimulus size. The range of stimulus sizes tested was normalized within each subject. (**C**) Proportion of correct responses for a fixed stimulus size (1.5′) as a function of drift diffusion constant across subjects. Error bars for proportion correct represent sem. (**D**) Visual acuity thresholds as a function of the diffusion constants measured during sustained fixation on a marker for 9 subjects (note, one subject was removed due to too few fixation trials).

time. For each observer, the target was maintained in this region for a duration comparable to or above the amount of time necessary for high acuity performance to plateau for high contrast stimuli[25,26] (mean ± std; 378.5 ms ± 62 ms). Additionally, individual's average gaze offset from the center of the target was not correlated with acuity (p = 0.751, r = -0.12).

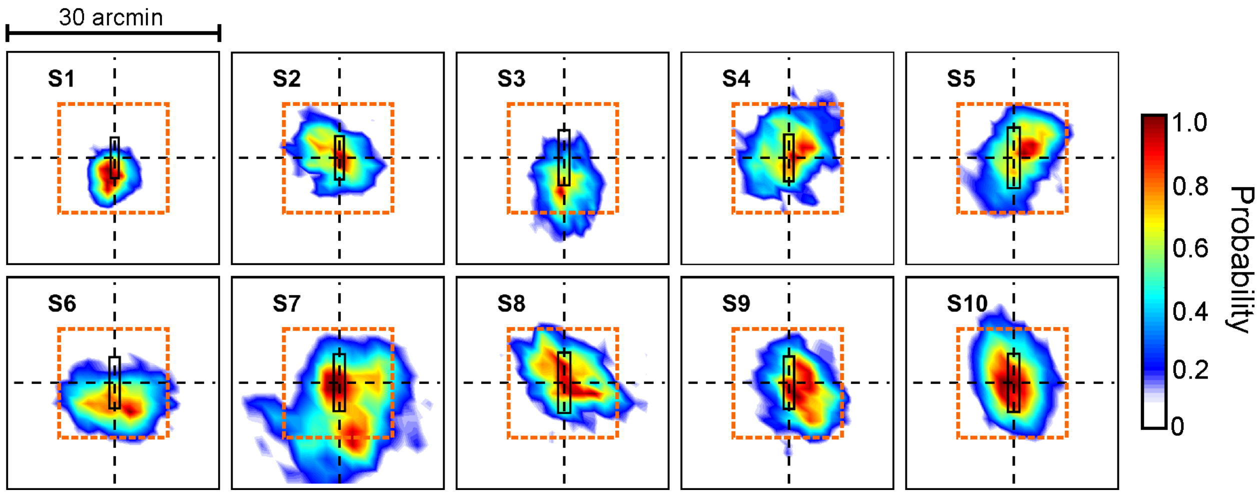

Figure 4: **Gaze position during the task.** Normalized 2D probability distributions of gaze position during stimulus presentation. Orange boxes delimit the central $16'$x$16'$ region. In each graph the central rectangle represents the stimulus size at their threshold acuity.

To better quantify the impact of ocular drift on acuity, we examined the changes in input luminance introduced by drift. To this end, we calculated the total power of these luminance changes for each subject and each digit (given a $1.5'$ width) used in the task (see methods for details). Since the total power yielded varied greatly across digits, the calculated power was normalized across subjects, separately for each digit. Fig.5A shows individual subjects' performance as a function of the total power conveyed to the retina averaged across the four digits. The overall input power was higher for subjects characterized by higher performance in the task and smaller drift diffusion constants ($p = 0.017$, $r = 0.728$). Performance, with a same size stimulus, decreased by approximately 29$\%$ for the subject with the least amount of power. To illustrate how the incoming visual flow to the retina differs for subjects with small vs. large drift diffusion constants, Fig. 5B show the power of the stimulus for a theoretical small and a large drift diffusion constant, respectively. A smaller diffusion constant sharpens the edges of the stimuli to a greater extent, making it easier to discriminate across stimuli (see also Supplementary Fig.5 and Supplementary Movie 1). Therefore, differences in the pattern of ocular drift well explain the observed changes in high-acuity vision across subjects; smaller drifts increase the power in the frequency range that is crucial to resolve high-acuity stimuli.

Discussion

Our results show that the pattern of ocular drift varies greatly across observers, and that these differences significantly affect the frequency content of the visual input experienced by individual subjects. Importantly, these behavioral differences are accompanied by corresponding individual differences in visual acuity: emmetropic subjects with smaller ocular drift can resolve finer detail. This finding is consistent with the characteristics of the

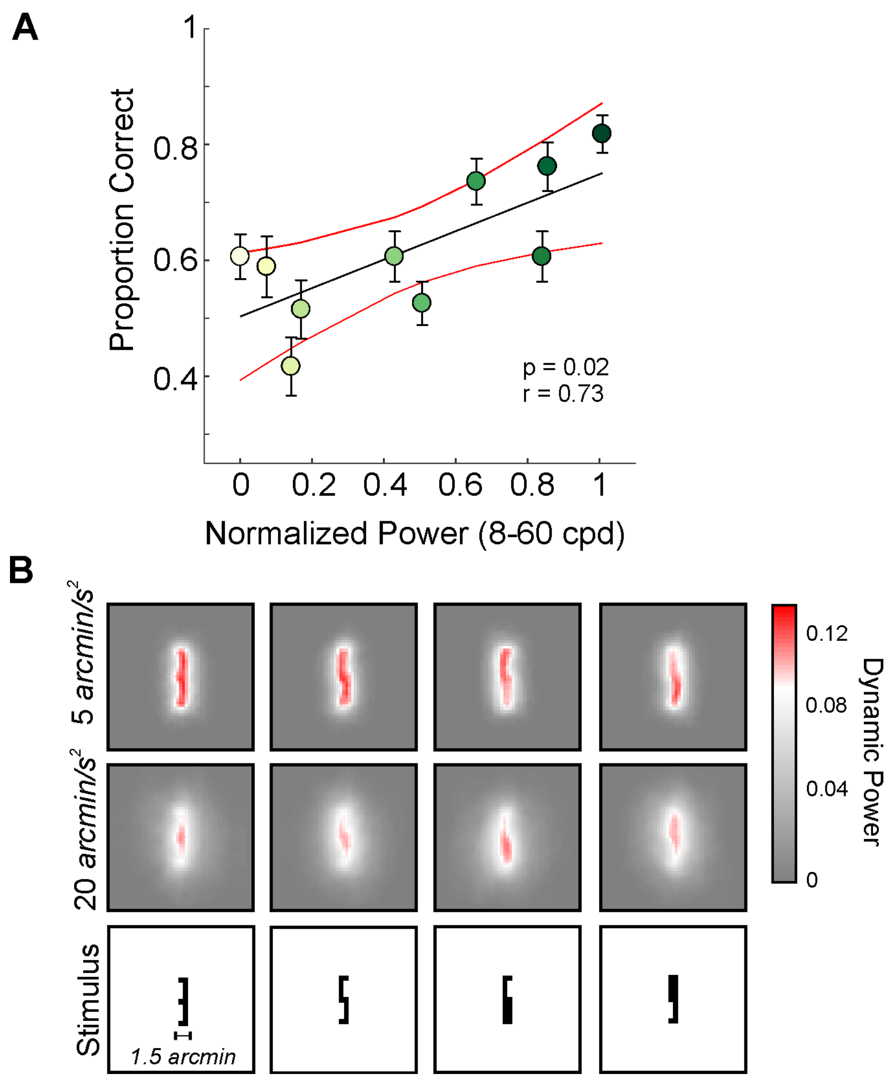

Figure 5: **Drift induced modulations of the retinal input during the task.** (**A**) Performance in the task as a function of total power conveyed to the retina (averaged across digits 1.5′ wide). Each circle represents a subject. Error bars represent 95% confidence intervals. (**B**) Power of the retinal input for a theoretical drift with small and large drift diffusion constant respectively (top rows), and the stimulus input (bottom row).

spatiotemporal luminance signals resulting from ocular drift; smaller drifts shift these signals toward higher spatial frequencies[8,5,12]. The physiological instability of the eye during fixation is generally ignored both in clinical and experimental evaluations of acuity. However, here we show that a clear relationship exists between the limits of high-acuity vision that an individual can achieve and their pattern of drift. Our findings should therefore prompt both scientists and clinicians to consider ocular drift when assessing vision.

These results are robust; the reported relationship between the amount of ocular drift and acuity is independent from the method used to measure high acuity. Indeed, we found the same relationship whether using the traditional Snellen Chart or a more controlled psychophysical method with stimuli viewed in isolation. Additionally, the same relationship between ocular drift and acuity was also found when ocular drift was measured in a simple oculomotor task that involved no measurement of acuity in which subjects maintained fixation on a marker. This finding indicates that these results can be reproduced under different conditions. A simple Snellen Chart test on emmetropic subjects can potentially inform us about their oculomotor behavior at fixation. Similarly, oculomotor behavior measured during a simple fixation on a marker can predict visual acuity. The implications of these findings are therefore far-reaching; ocular drift can predict acuity and vice versa.

Notably, the existence of a correlation between ocular drift and high-acuity vision does not imply causation. Differences in acuity may lead to changes in ocular drift, as well as vice versa. While theoretically, (assuming a static eye) the limits of high-acuity vision are dictated by cone spacing in the central fovea[27,14,16], in practice eye optics also pose an unavoidable bottleneck by effectively limiting the highest frequency that can be resolved[14,28,27,18]. Individuals characterized by a tighter cone spacing and fewer optical aberrations can potentially resolve higher spatial frequencies, and will benefit the most from a smaller drift motion when compared to individuals with more pronounced optical aberrations and/or wider cone spacing. For observers with lower acuity due wider cone spacing and/or optical aberrations, a reduction of ocular drift motion may not lead to a substantial advantage. This work highlights how ocular drift is an important component in the equation explaining humans' ability to achieve high acuity vision, and opens many questions regarding how the interplay of ocular drift with optics and anatomical factors unfolds. Here we argue that ocular drift represents another equally substantial influence on individual's ability to achieve high acuity by modulating the range of spatial frequencies that are maximally enhanced in the visual input[8,5,12].

Based on the results presented here, demonstrating that smaller drift motion is associated with higher acuity, we may be drawn to conclude that the absence of ocular drift, *i.e.* perfect image stabilization, would be the most beneficial condition for high-acuity vision. This however is not the case; multiple studies have already shown how retinal stabilization decreases performance in high-acuity tasks[10,8,5,9]. These findings are consistent with the response characteristics of neurons in the early stages of the visual system. In the absence of other forms of temporal modulations, eliminating drift motion entirely will concentrate all power of the retinal input at 0 Hz. This effect is expected to lead to an overall decreased neural response, as neurons are mostly sensitive to non-zero temporal frequencies[19,29].

Note, however, that while an absence of retinal motion actually impairs vision, much smaller amounts of drift than those measured here could potentially enhance high-acuity vision further. Therefore, why is drift motion not further minimized? It is possible that achieving higher control over drift is beyond the capabilities of the humans' visuomotor system. Yet, even if the system is capable of reducing drift further, this may not be beneficial. Progressively smaller drifts will enhance even higher spatial frequencies beyond 60 cpd while simultaneously dampening the power of frequencies below this limit (See Fig1C). This would result in reduced power in the visible frequency range, while enhancing power in a range beyond what humans can possibly resolve. Therefore, further reducing drift motion also has disadvantages, particularly if we consider that visual stimuli falling on the central fovea are generally characterized by both low and high spatial frequencies, all of which may be equally important to discriminate depending on task requirements.

Previous work has shown task-dependent changes in drift characteristics[30]. Recent work has also shown that individuals express differences in ocular drift movements across various conditions, especially when looking at different types of stimuli[8,31], and when the head is free[32]. While there is evidence indicating that highly trained subjects are characterized by more stable fixation[3], and drift can be actively modulated depending on the viewing condition[8], it remains unclear if ocular drift can change with training and experience. In light of the findings reported here, understanding if ocular drift can be shaped through training has important clinical and practical implications, potentially allowing for improvements in high-acuity vision.

Importantly, even if cone spacing and optics allow for resolution of frequencies up to 60 cpd, our findings indicate that in theory certain patterns of ocular drift can decrease the power in the very high frequency range (See Fig. 1C), effectively setting the visual acuity limit. Ultimately, it is unlikely that any one of these factors alone determines acuity, but rather acuity is the outcome of the interplay of oculomotor behavior, optics and anatomy at this scale, and further research is crucially needed to elucidate the interplay of these factors.

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Methods and Procedures

Observers. 10 adult observers with normal vision participated in this study. 9 naive subjects, and 1 experienced observer (Subject 2) who is an author. Subjects ranged in gender (3 males, 7 females) and age from 18 to 25 years old. All subjects except for the author were emmetropic and required no correction to reach a minimum of 20/20 Snellen acuity. The author wore corrective contact lenses. This research study was approved by the University of Rochester's Research Subjects Review Board. Subjects were invited for an initial screening session, which involved a thorough explanation of the experiment, as well as a detailed review of the materials in the consent form. After the subject understood the information in the consent form and verbally agreed to participate in the study, informed consent was obtained and documented.

Stimuli and Apparatus. Stimuli were presented monocularly to the right eye while the left eye was patched. Eye movements were recorded with high precision either by means of a Generation 6 Dual Purkinje Image (DPI) eye tracker (Fourward Technologies), with a 1kHz sampling rate[33,20], or by means of custom-made digital Dual Purkinje Image (dDPI) eye tracker, with a sampling rate of 340Hz[34]. Both systems have an internal noise well below $1'$, and a spatial resolution of at least $1'$[33,20]. To reduce noise and achieve higher precision in the eyetracking signal, the head was immobilized by means of a dental-imprint bite bar and head-holder. Stimuli were shown on a LCD monitor (ASUS PG258Q), with a vertical refresh rate of 200Hz, and a spatial resolution of 1920 x 1080 pixels. The monitor was between 3 or 5 meters away from the observer (1 pixel = $0.25'$ and 1 pixel = $0.19\ '$, respectively).

Stimuli consisted of 3,5,6 and 9 digits from the Pelli number-font[23]. These targets were presented in isolation at the center of the display (emphasized using peripheral arches) for 500 ms. Conveniently, these stimuli also allow us to compare performance in isolation with performance under crowded conditions in the fovea, overcoming issues that would normally arise when using traditional optotypes[23]. Stimuli consisted of black font presented on a gray background. Stimuli were rendered by means of EyeRIS[21], a custom-developed system allowing flexible gaze-contingent display control. This system acquires eye movement signals from the eye-tracker, processes them in real time and, if necessary, updates the stimulus on the display according to the desired combination of estimated oculomotor variables.

Experimental Paradigm. Data were collected by means of multiple experimental sessions. Each session lasted approximately 1 hour, and each subject completed on average 5 sessions. Every session started with preliminary setup operations that lasted a few minutes, involving comfortably positioning the observer in the apparatus, tuning the eye tracker for optimal performance, and executing a two-step gaze-contingent calibration procedure to map the eye tracker's output into visual angle. This procedure improves localization of the preferred retinal locus of fixation by approximately one order of magnitude over standard methods[22]. In the first phase (automatic calibration), observers sequentially fixated on each of the nine points of a 3×3 grid, as it is standard in oculomotor experiments. Points in the grid were 1 or 1.25° apart from each another on the horizontal axes, and 40 or $50'$ on the vertical axes (varying based on screen distance). In the second phase (manual calibration), observers confirmed or refined the mapping given by the automatic calibration by fixating again on each of the nine points of the grid while the location of the line of sight estimated on the basis of the automatic calibration was displayed in real time on the screen. Observers used a joypad to fine-tune the predicted gaze location if necessary. The manual calibration procedure was repeated for the central position before each trial to compensate for possible microscopic head movements and system drift that may occur even on a bite bar.

Once the subjects initiated the trial, a brief $10\times10'$ fixation point was presented at the center of the screen to clearly identify the location where the stimuli would appear. A 400ms delay period followed the blank screen to avoid any aftereffects from the fixation point. The target was then presented. Subjects were asked to identify the stimulus, choosing among 4 possible digits, by pressing a button on a remote controller. Trials in which subjects were required to maintain fixation on a $10\times10'$ marker (fixation trials) at the center of the display were presented once every 30-50 task trials. In fixation trials subjects were instructed to maintain fixation for 2-5 seconds.

Target acuity was determined by following the Parametric Estimation by Sequential Testing (PEST) procedure[35], according to which, size would change online based on subject performance.

Data Analysis

Eye Movements. Eye movements were categorized into two main groups: saccades (including microsaccades) and ocular drift. Ocular motion in between saccades was defined as drift. Classification of these eye movements was first performed automatically, then thoroughly reviewed by an expert experimenter. Trials containing saccades, blinks and/or bad tracking during stimulus presentation were removed. Furthermore, trials in which subjects did not respond or gaze was more than 30′ from the center fixation point at the beginning of the trial were also removed (on average 1.3% ± 0.58% of the total trials) . We characterized ocular drift using the diffusion constant. Diffusion constant was determined based on the empirical average 2D eye displacement as a function of time for time lags ranging from from 50 to 256 ms. Eye displacement data was then fitted with a linear regression and the diffusion constant was calculated as the slope of the fitted line divided by 4. Deviations from the fit were minimal for all subjects.

Estimation of Acuity Thresholds. Visual acuity threshold, *i.e.* the minimum stimulus width required to perform reliably above chance level (62.5% correct,with a 25% chance level), was determined using a cumulative Gaussian psychometric function[36].

Power Spectrum analysis. The power spectrum of the luminance modulations delivered by ocular drift to the retina was estimated based on each subject's drift diffusion constant following the method described by Intoy and Rucci[8]. The drift dynamic power was calculated by summing across all non-zero temporal frequencies of the drift power spectrum (see Fig. $5A$) multiplied by the power spectrum of the external stimulus (for stimuli of 1.5′ in width). To quantify individual differences, we summed the resulting power spectrum across all spatial frequencies between 8-60 cpd, *i.e.*, the most informative range of spatial frequencies for discriminating across stimuli. This operation was performed for each subject and for all digits used in the task. In Figure $5B$, the plotted power was normalized per each digit across subjects. The normalized power was then averaged per each subject.

All data and MATLAB scripts used to create the figures in the manuscript have been uploaded onto the Open Science Framework repository.