Is ocular drift controlled to enhance perception?

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1 Introduction

Even while fixating on a single interesting location, our eyes continue to slowly wander with a movement known as ocular drift. Recent studies show that ocular drift facilitates high acuity vision (Rucci et al. 2007, Boi et al. 2017, Ratnam et al, 2017), but it is not known whether drift is tuned according to the demands of the visual task.

A Brownian motion model of drift suggest that it acts a filter to amplify high spatial frequencies which have low power in natural visual scenes (Kuang et al. 2012). This model also suggests that reducing the diffusion constant of drift extends the amplification to higher spatial frequencies (see note on Janis's wiki page).

This raises the hypothesis that drift will change to increase power on the retina if needed. Sensitivity in different amounts of drift may be predicted by the power on the retina provided by Brownian motion processes.

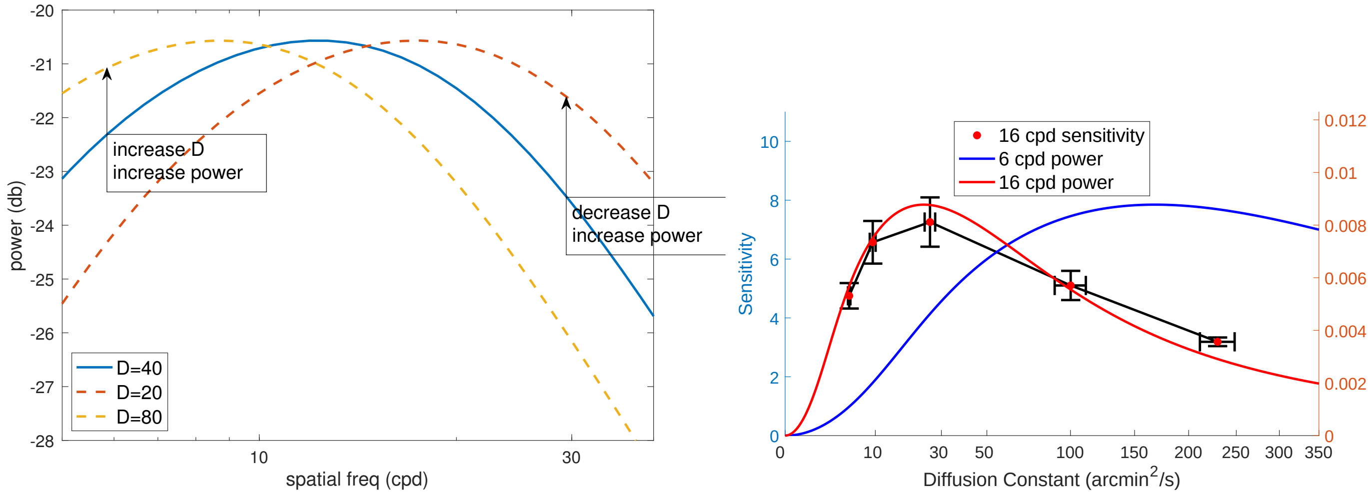

Figure 1: **Theoretical rationale for main hypotheses. (LEFT)** Drift of different diffusion constants (D) amplify different ranges of spatial frequencies when the average temporal sensitivity of retinal ganglion cells is taken into account (see Janis's notes on Brownian motion models in Drift Gain project). Larger diffusion coefficients enhance low spatial frequencies (yellow) and smaller diffusion coefficients enhance higher spatial frequencies (red) compared to "normal drift" (blue). **(RIGHT)** Power preferred by the retina for different amounts of drift and 2 different spatial frequencies (red and blue solid curves). Data are from the 16cpd drift gain experiment (with scotoma) and match well the theoretical curve for 16 cpd (red curve). The blue curve predicts that larger drifts are more beneficial for the low spatial frequency (6cpd).

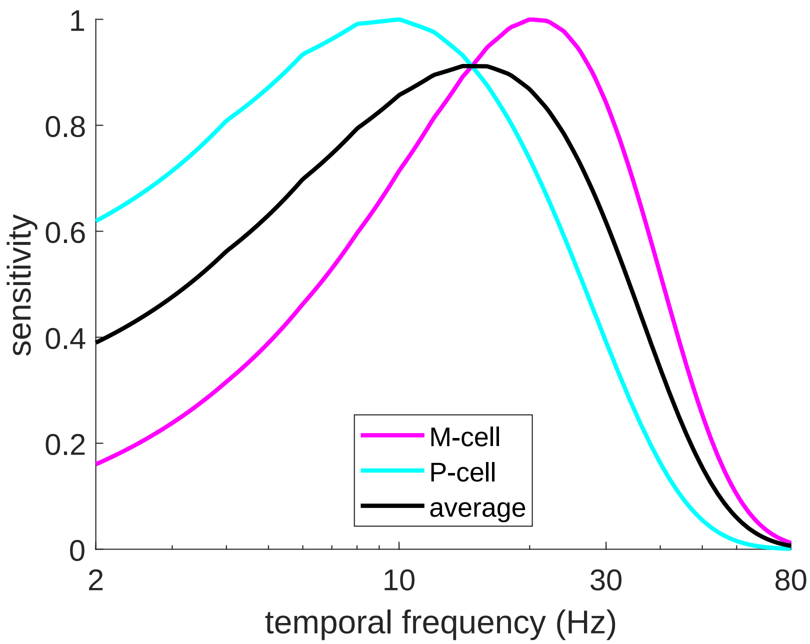

Figure 2: Retinal sensitivity profiles from Benardete and Kaplan (1999ab). The black line shows the average sensitivity of the two cell types.

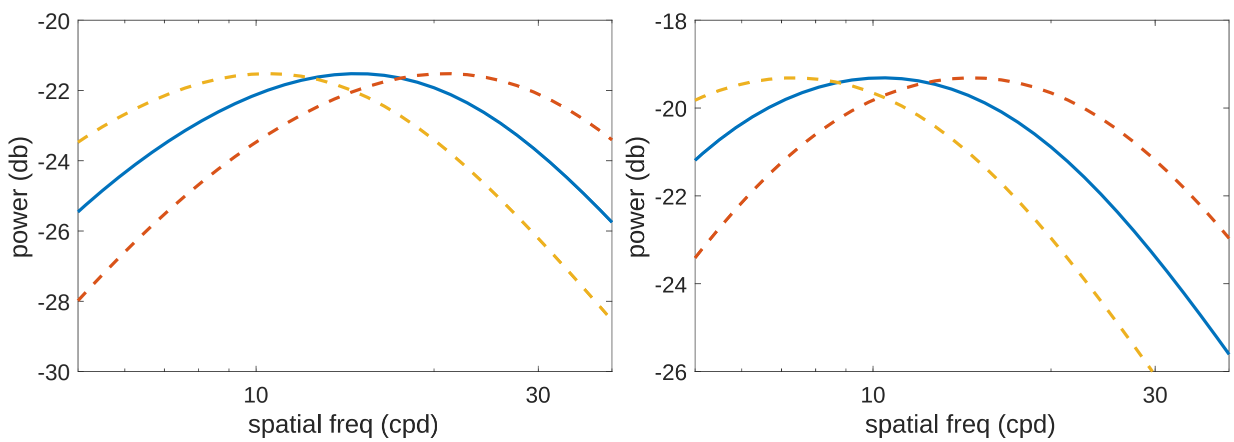

Figure 3: Left: Prediction by M-cell sensitivities (left) and P-cells (right).

2 Fixation vs. 16 cpd

Comparison of drift in during the 500ms fixation period and the 500ms plateau period of the drift gain experiment (gain = 1, scotoma on) suggest that drift characteristics change between the conditions. This is consistent with results from the Snellen test (see 4).

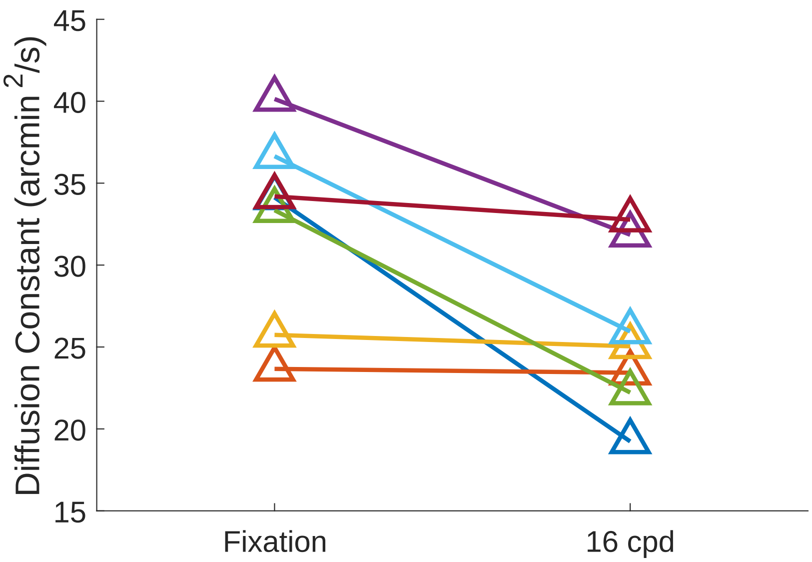

Figure 4: Diffusion constants of seven subjects during fixation and extra-foveal examination of 16 cpd grating are significantly different. Wilcoxon signed-rank test $p = 0.156$.

3 Experiments

3.1 Experiment 0: 6cpd with scotoma to accompany original study

Repeat original study at 16cpd with 6 cpd - scotoma on, gains = 0, 0.5, 1, 2, 3, ... This could be combined with Experiment 2 which proposes the same experiment but in the fovea.

3.2 Experiment 1: Does drift change to modulate temporal power on the retina?

Here I suggest comparing oculomotor behavior in an orientation grating discrimination task using 6 and 20cpd gratings at 65% and 90% performance thresholds.

- Task: 2AFC grating orientation discrimination ($\pm 45°$)
- stimuli have a gaussian envelope - mask will show after stimulus offset
- Two psychometric curves will be estimated for each subject - one at 6 and one at 20cpd.
- Pest will be alternately set in blocks to target either 65% or 90% performance so that data is collected in a large range of contrasts
- Add a mask after stimulus offset

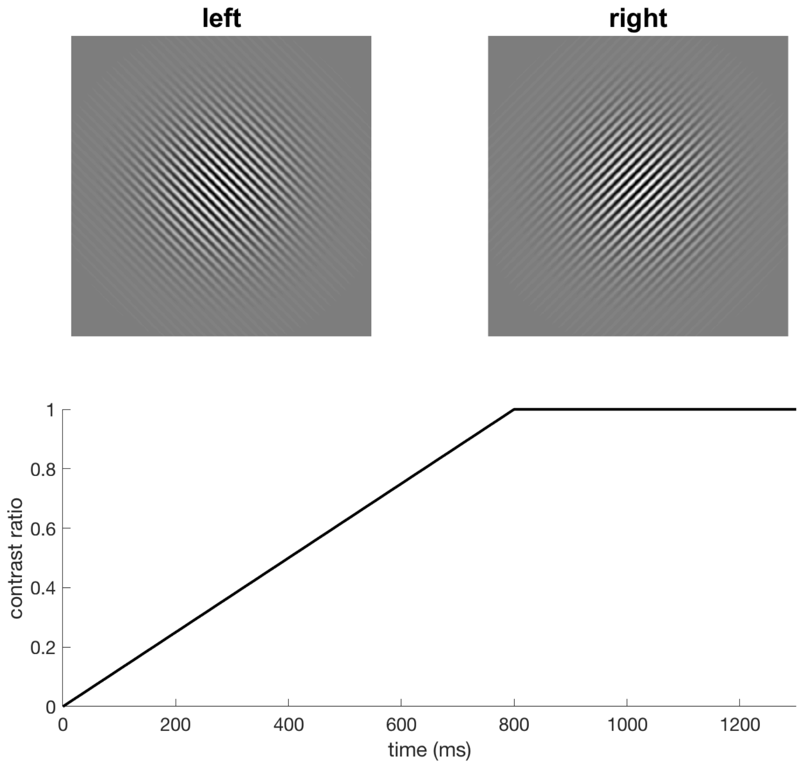

Figure 5: Stimuli for 2-AFC task and contrast ramp in a single trial. 6SD of the gaussian envelope cover about 6.5 degrees.

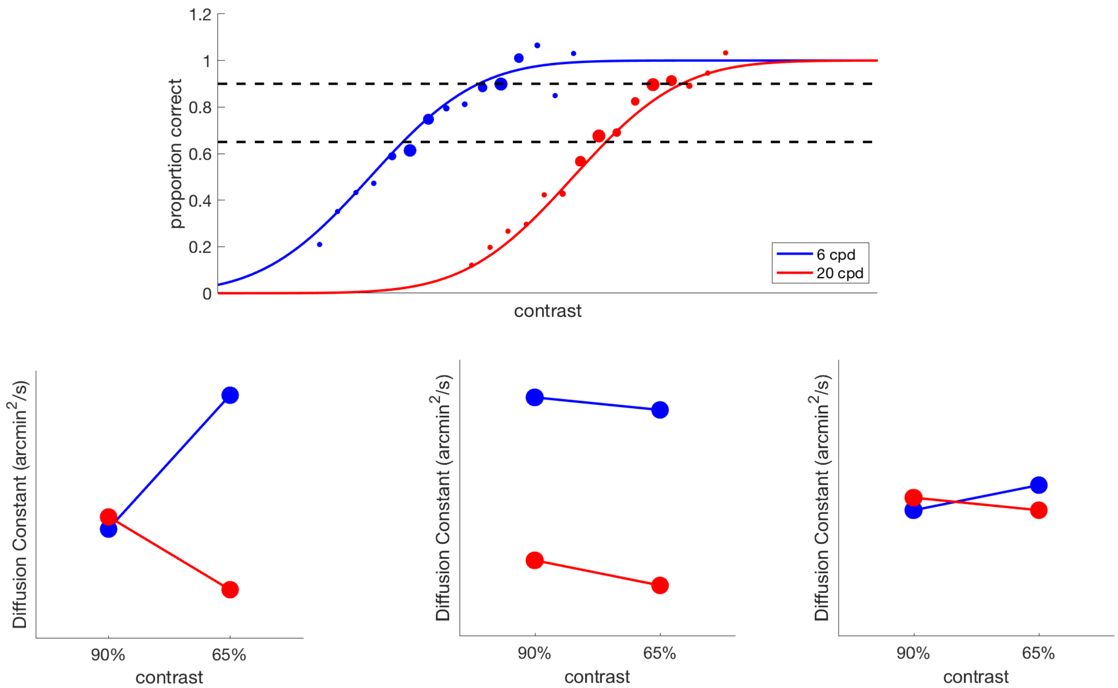

Figure 6: **Expected Results**. Psychometric functions will be fit for both 6 and 20 cpd. Data near each threshold will be aggregated to compute the diffusion constants in the 4 conditions (6 or 20 cpd by 90% or 65% threshold). Possible results: (LEFT): For a high contrast stimulus (when the stimulus provides high retinal power), drift diffuses at some normal level, possibly similar to what occurs during sustained fixation. When the contrast of the stimulus is reduced, drift changes as needed towards 'optimal', which for high and low spatial frequency stimuli go in opposite directions. (MIDDLE): If drift diffusion is driven by the spatial frequency present in the stimulus, regardless of power, we may see different diffusion constants invariant to the contrast of the stimulus. (RIGHT): Negative results - no change in diffusion constants. In this case we should definitely do the drift gain study (Experiment 2) to test whether performance can be optimized by maximizing power on the retina.

3.3 Experiment 2: Does power from Brownian motion predict sensitivity for different amounts of motion?

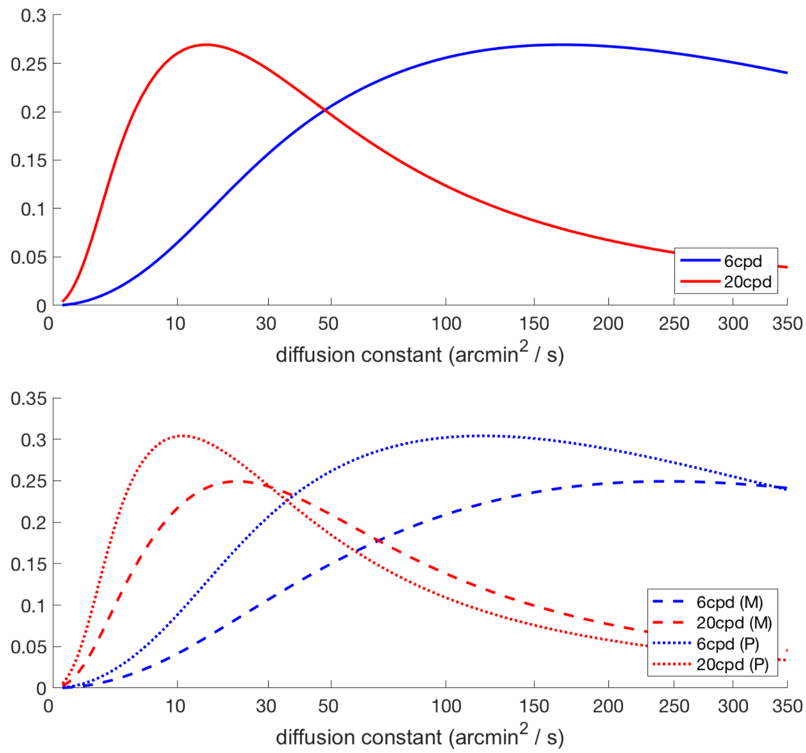

Figure 7: Temporal power preferred by the retina for the average of M and P cells (top) or the individual neuron types (bottom)

Whether or not drift does change as hypothesized in section 3.2, here we test whether sensitivity is proportional to the temporal power available in the fovea (Example predictions in 1, right). For a subject whose natural behavior is already optimal, we would expect to see that sensitivity falls when retinal image motion is manipulated. For a subject whose behavior is not optimal, we may find a gain that can improve his/her sensitivity based.

If there are large changes in normal diffusion constants between subjects, gain conditions could be determined for each individual to have an ideal spread of diffusion constants to compare with the prediction.

Here we measure sensitivity for several gain conditions (0, .5, 1, 2, 3) at both 6 and 20 cpd and compare to the power predicted. Depending on the normal behaviors of the subjects, we may expect that sensitivity is improved for 6cpd and gains > 1.

3.4 Experiment 3: Predictions based on individual temporal sensitivity

To individualize predictions we should measure the temporal sensitivity of individual subjects *foveally* under stabilization for both 6 and 20 cpd (repeat Kelly, 1979). Ideally this would be done by measuring full psychometric functions for several combinations of spatial and temporal frequencies (and eccentricities for Experiment 4). However, to do this quickly, we can use a method limits and let the subject decide when the stabilized, sinusoidally modulated (or drifting) grating is barely visible. Subjects will be asked to fixate a central marker during this procedure to help with fixation and use buttons on the joypad to increase or decrease the contrast of the stimulus. We can repeat this procedure 4 times (2 times ascending, 2 times descending) and get an average threshold. (or more if the procedure is fast enough). The orientation of the grating can vary between these repeats.

Proposed conditions: [6cpd, 20cpd] by [0Hz, 2Hz, 5Hz, 10Hz, 16Hz, 24Hz] = 12 total conditions

Technical concern: Can we reasonably quickly update the contrast of a modulated stimulus on the fly?

3.5 Experiment 4: Measuring spatiotemporal sensitivities across the retina

This experiment generalizes on Experiment 3 to other spatial frequencies and eccentricities. To isolate eccentricities, a grating confined to an annulus around the center of gaze.

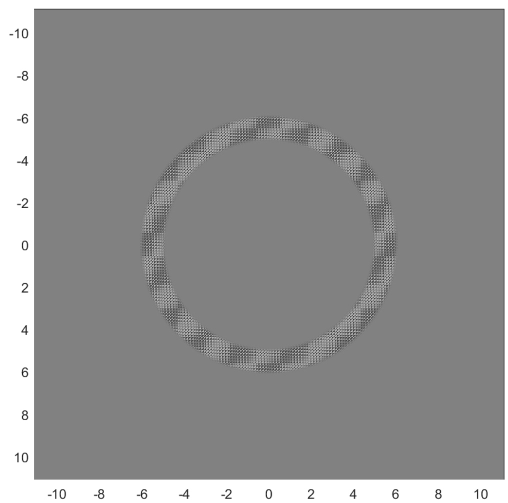

Figure 8: Example of grating in annulus at 5° eccentricity. (I apologize for the aliasing).

Proposed conditions: [2cpd, 6cpd, 10cpd, 20cpd] by [0Hz, 2Hz, 5Hz, 10Hz, 16Hz, 24Hz] by [0deg, 1deg, 2deg, ..., 7deg]
Eccentricity range will be constrained by monitor.

4 Other Observations

4.1 Drift in different tasks

Here I compare diffusion constants measured from subjects in several different tasks, categorized loosely into fixation, natural viewing, and high acuity tasks. The diffusion constants for the high acuity tasks (small face viewing and Snellen acuity task) are the smallest on average. Reading seems on par with the high acuity tasks so perhaps it could be reclassified, though it seems to have a larger spread of values (I will double check the font size used in the task).

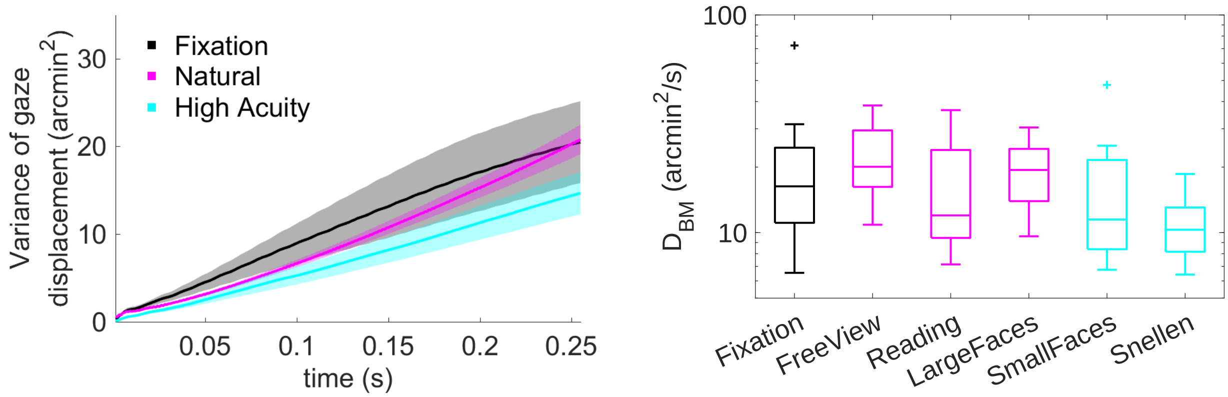

Figure 9: Diffusion constants in different viewing tasks. Fixation: N=12, FreeView: N=9, Reading: N=13, LargeFaces: N=15, SmallFaces: N=10, Snellen: N=8

4.2 Rania's Data

Rania recorded data on herself in a grating discrimination task (spatial frequency unspecified but probably low - 1cpd maybe?) at three different contrast levels. Her performance seemed to be above chance at all three levels, and the diffusion constant of her drifts seemed to change systematically:

	Contrast Level		
	0.1	0.25	2
MS Rate (#/s)	0.9±0.2	0.8±0.1	1.0±0.2
MS Amp (arcmin)	14.5±0.4	15.1±0.4	13.8±0.4
Drift Duration (ms)	508.7±26.4	578.2±28.2	455.6±21.6
Drift Span (arcmin)	6.1±0.1	4.2±0.1	10.7±0.1
Drift Speed (arcmin/s)	39.2±1.1	37.9±0.7	63.1±19.3
Drift Curvature (arcmin^{-1})	120.4±82.5	40.9±7.2	30.3±2.0
Diff Constant (arcmin^2/s)	16.4	17.7	33.1
Performance	62%	90%	100%

4.3 Grating Detection Task by Sara

Full report available on Sara's project page on the wiki.

Sara ran a grating detection study in which a 8cpd grating was tilted to the left or right with the hypothesis that drift would behave differently for the two orientations. She did not find any significant differences in behavior between the two conditions but this data could be a good starting place to explore different types of analyses:

- curvature instead of curvature index
- full instantaneous velocity characterization
- diffusion constant estimation (with a directional bias term)
- comparison of low versus high contrast trials (regardless of orientation)

4.4 Other databases

Giorgio's CS data, Christie's data, Nagmeh's data,...

5 Relevant Literature

- Cherici et al (2012) - Precision of sustained fixation in trained and untrained observers
- Epelboim & Kowler (1993) - Slow control with eccentric targets: Evidence against a position-corrective model
- Poletti et al (2015) - Head-Eye Coordination at a Microscopic Scale