Drift Gain: On Retinal Amplification

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Contents

Summary: Here I improve upon two points in our model of the retina and correct a previous error about retinal amplification.

1. Remove (or rather reduce) the assumption that the retina is NOT sensitive to temporal frequencies < 2Hz.

2. Incorporate an anatomically plausible ratio of P:M cells in the temporal sensitivity of the retina in the region where the stimulus was presented.

1 Introduction

In previous reports we have applied a retinal amplification factor (1.46) to drift when estimating diffusion constants and modeling Brownian motion to account for rotations around the center of the eye instead of the optical nodal point. However, this amplification also applies to the image that impinges on the retina. Therefore, we need to compute temporal power in external image coordinates or in retinal coordinates.

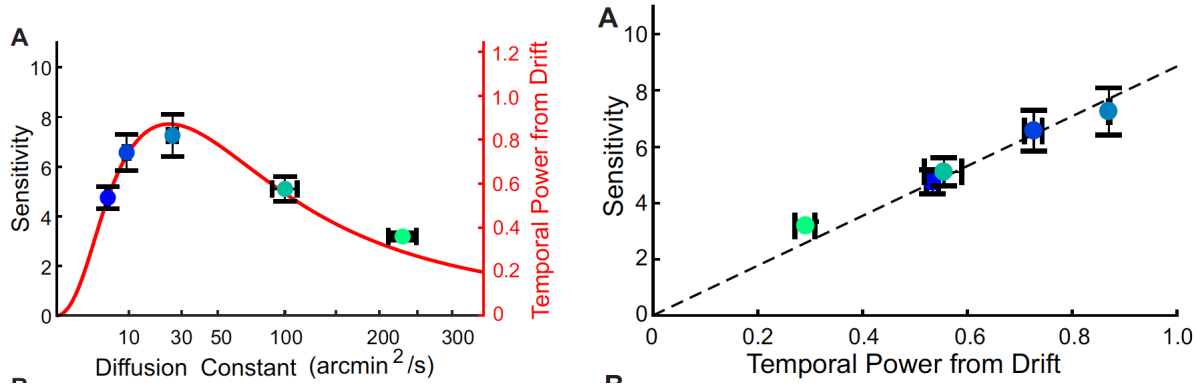


Figure 1: Predictions and sensitivities when retinal amplification factor has been applied to the observed diffusion constants, but *not* to the retinal image of the grating.

$$D_R = 1.46^2 D_E$$

where D_E is the diffusion constant of the eye around the nodal point. A stimulus of k cycles per degree in the world would have $k_R = k/1.46$cpd on the retina.

1.1 Important Notes

$$S(k = 16; D_R) = \int_2^{80} Q(k = 16, f; D_R)\,[5 \cdot H_P(f) + H_M(f)]\; df$$

where H_P and H_M are the temporal sensitivities of P and M cells respectively (fig 3). The temporal senstivities of P and M cells are as described by Benardete & Kaplan 1999ab.

Important notes about the current model version:

- We make the assumption that the retina is not sensitive to temporal frequencies < 2Hz.

- The temporal sensitivity function is an average between the M and P cell sensitivities, where these were somewhat arbitrarily combined by normalizing each to their max before averaging. This type of average suggests a P:M cell ratio of about 5.
- I am certain the brownian motion model and diffusion constant estimation are correct - I've double checked and details are in Janis's notes: `https://wiki.bcs.rochester.edu/ApLab/Projects-Janis-Brow`

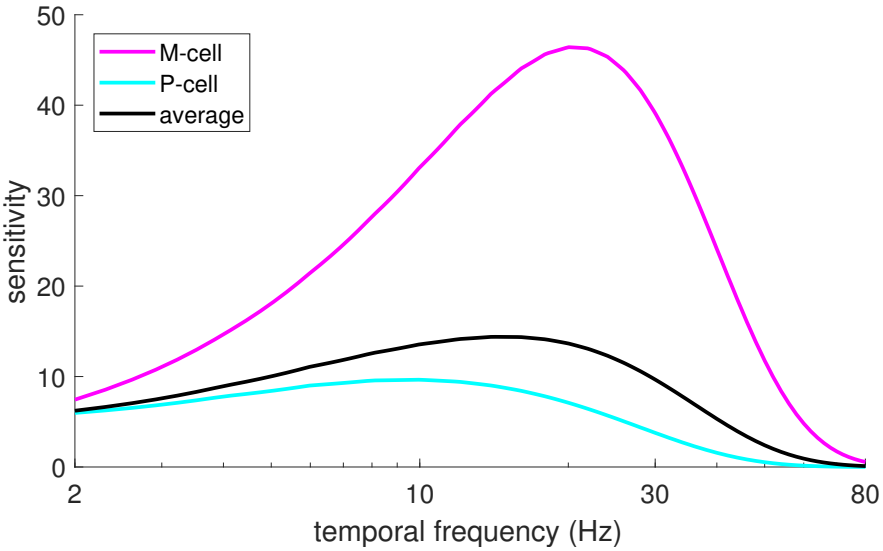


Figure 2: Sensitivity of retinal cells and their average when weighted with a 5:1 P:M cell ratio. (Note that at 5deg eccentricity, this P:M cells ratio is about 10). The average sensitivity (black) used previously integrated over frequencies (2-80Hz).

2 Same model, removing retinal amplification factor from D

1. External coordinates: The retinal amplification factor modulates the diffusion constant by a factor of $1.46^2 \sim 2.13$. In external image coordinates, this would shift all of the measured sensitivities in figure 1 to the left (smaller diffusion constants) and the temporal power curve remains the same. This would suggest that humans are moving less than 'optimal'.

2. Retinal coordinates: If we instead apply the retinal amplification factor to the grating, then the spatial frequency of the grating on the retina is 16/1.46 cpd - a smaller spatial frequency value. Relative to the data points in figure 1, this would move the peak of the temporal power curve to higher diffusion constants. Again, suggesting that humans are moving less than optimal. (figure 3)

Now we reconsider the diffusion constant and spatial frequency both in external coordinates. Temporal power:

$$S(k = 16; D_E) = \int_2^{80} Q(k = 16, f; D_E) \left[5 \cdot H_P(f) + H_M(f)\right] / 6 \, df$$

where H_P and H_M are the temporal sensitivities of P and M cells respectively (fig 3).

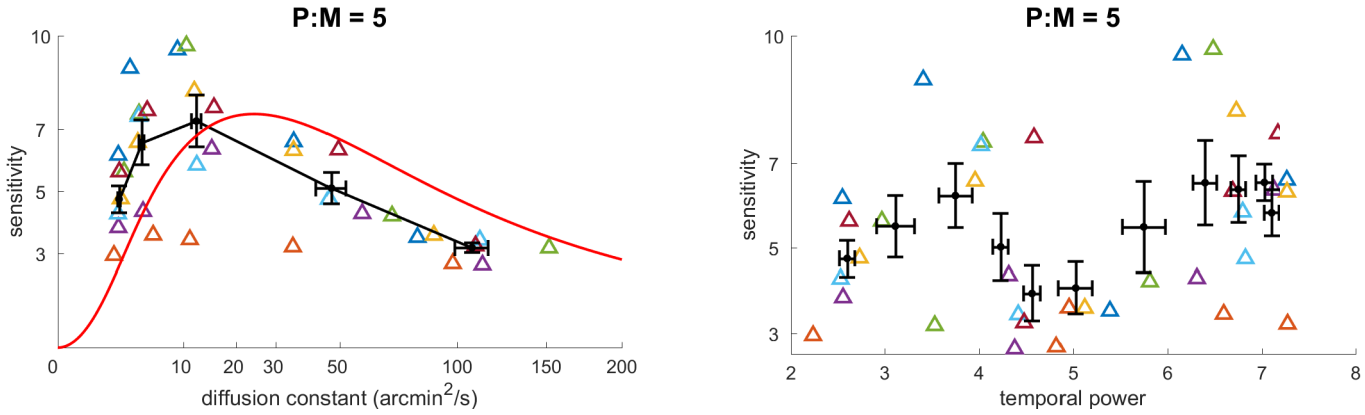


Figure 3: Sensitivity and model vs diffusion constant when the extrafoveal P:M cell ratio (5) is taken into account and power is integrated over 2-80Hz. LEFT: Black points with error bars are averages across subjects within gain condition. RIGHT: Black points with error bars are a sliding average over temporal power, with 7points in each.

3 Model Update: P:M anatomical ratio

$$S(k=16;D_E)=\int_{0.63}^{80} Q(k=16,f;D_E)\left[20\cdot H_P(f)+H_M(f)\right]/21\,df$$

where H_P and H_M are the temporal sensitivities of P and M cells respectively (fig 4).

One common suggestion has been to account for the **anatomical P:M cell ratio in the relevant region of the retina**. In the human retina at 5degree eccentricity, the P:M cell ratio is about 10 (Curcio and Allen, 1990; Dacey, 1993). A similar P:M cell ratio is found in the macaque retina (Perry and Cowey, 1985).[1] Closer to the fovea this ratio is likely larger, so here let's extrapolate that the P:M cell ratio is around 20 just outside of the fovea. (Recall also that the maximum temporal sensitivity of M cells is also ∼5 times higher than P-cells already. Benardete & Kaplan, 1999ab)

P-cells in particular have been shown to have a lowpass sensitivity. In weighing these more than M cells the sensitivity to low temporal frequencies is increased. **Here I remove the assumption that the retina is not sensitive to frequencies $<$ 2Hz and integrate over frequencies between 0.63-80Hz**[2].

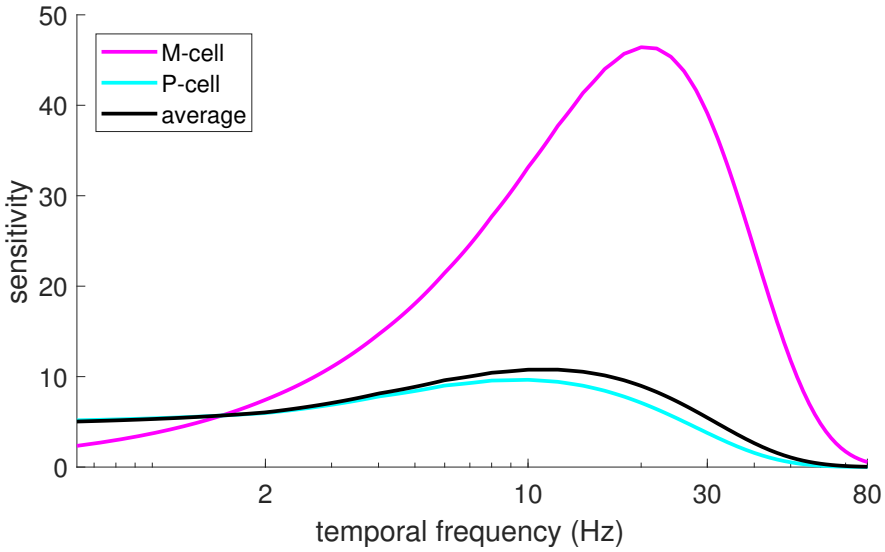


Figure 4: Sensitivity of retinal cells and their average when weighted with a 20:1 P:M cell ratio. (Note that at 5deg eccentricity, this P:M cells ratio is about 10). The average sensitivity (black) is used in this updated model (0.63-80Hz).

[1] See JI's notes on Peripheral Neural Sampling for more details.

[2] Starts integral in same place as Casile, Victor, Rucci model however, there is no reason not to start integrating at 0 because the spatiotemporal frequency content is estimated with a closed form equation (no aliasing)

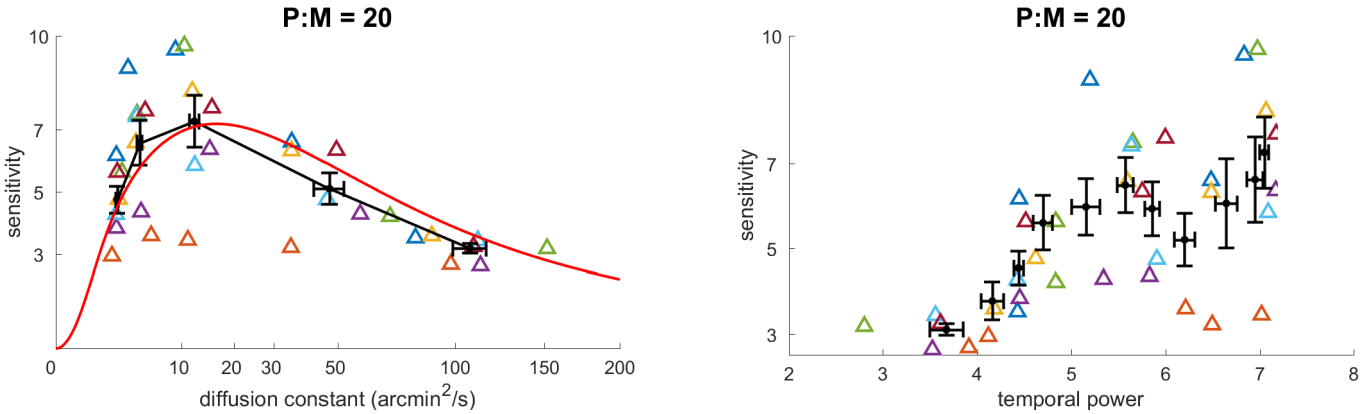
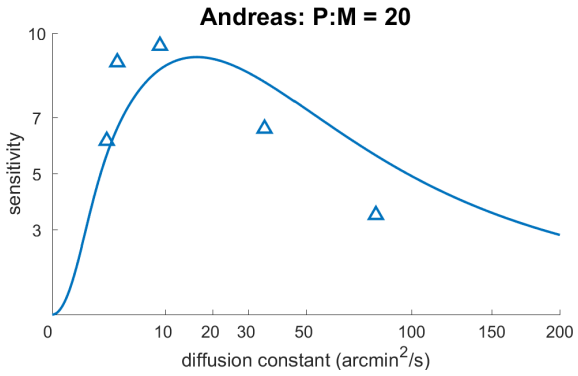
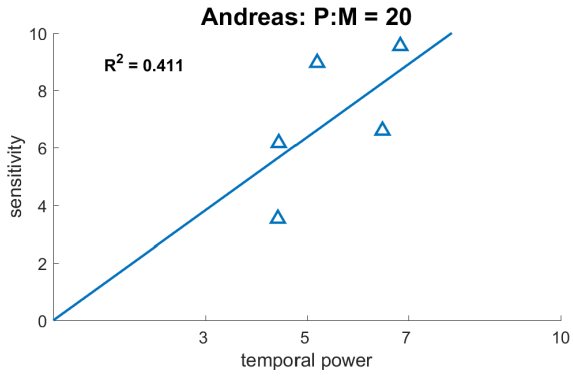
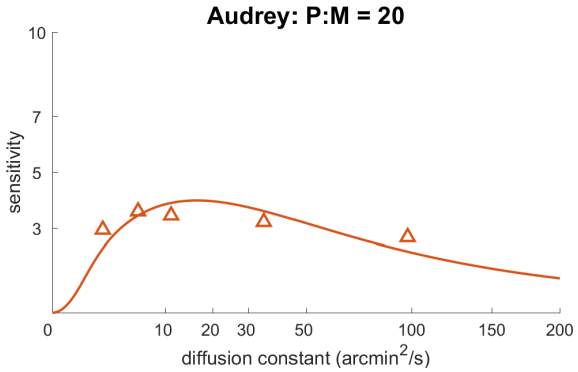


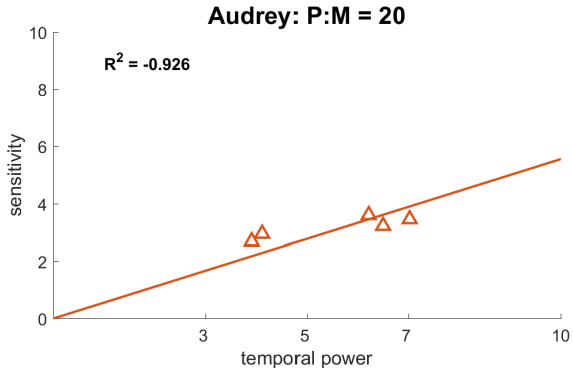
Figure 5: Sensitivity and model vs diffusion constant when the extrafoveal P:M cell ratio (20) is taken into account and power is integrated over 0.63-80Hz. (Note that in this example no normalization has been applied to account for intersubject variability)

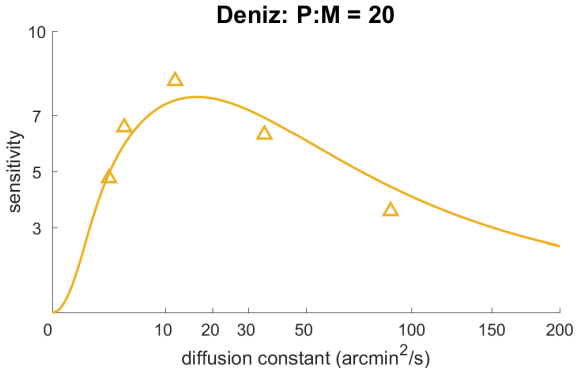
3.1 Individual Fits

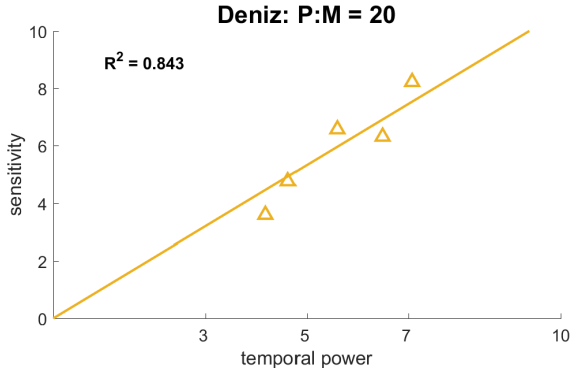


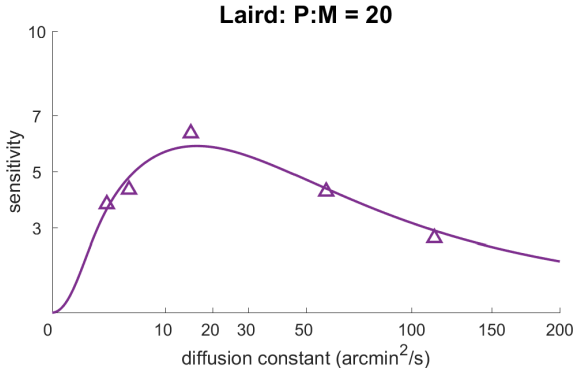


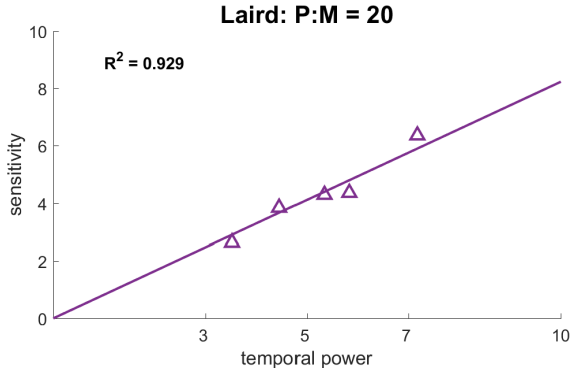


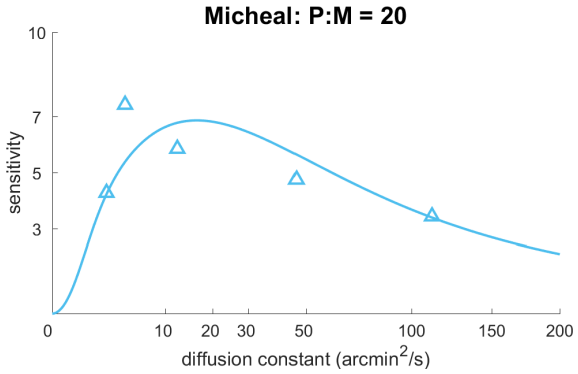








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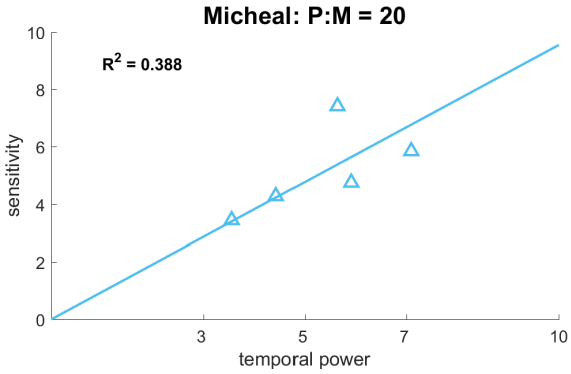
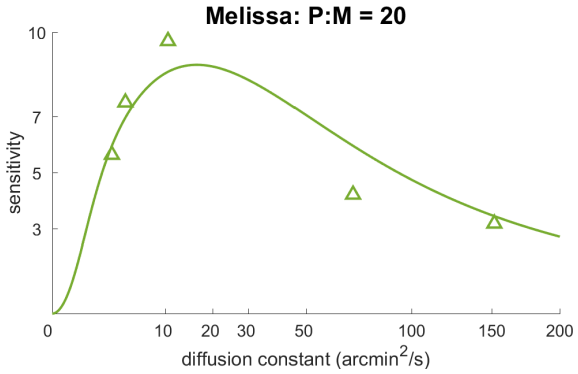
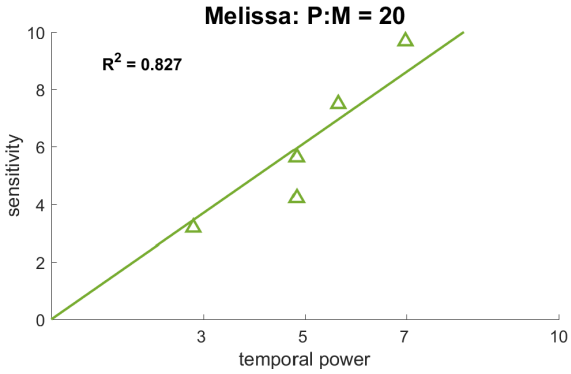
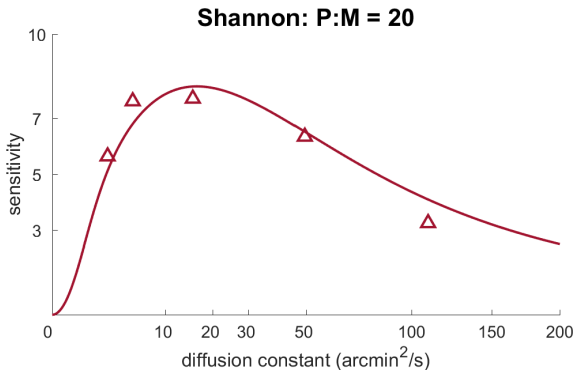
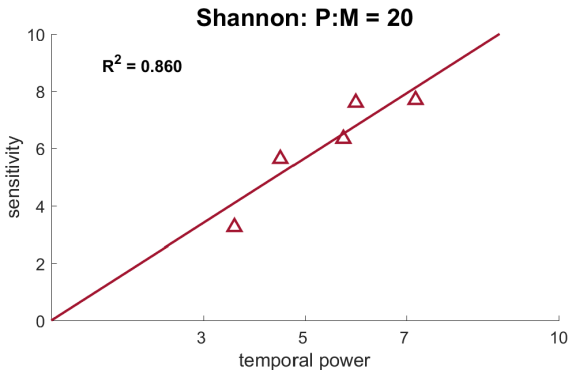
sensitivity
diffusion constant (arcmin^2/s)


Micheal: P:M = 20
R^2 = 0.388
sensitivity
temporal power


Melissa: P:M = 20
sensitivity
diffusion constant (arcmin^2/s)


Melissa: P:M = 20
R^2 = 0.827
sensitivity
temporal power


Shannon: P:M = 20
sensitivity
diffusion constant (arcmin^2/s)


Shannon: P:M = 20
R^2 = 0.860
sensitivity
temporal power

3.2 Optimal ratio of P:M cells

Here I compute the P:M cell ratio that optimizes the fit between the data and temporal power for both average data and individual data. If the relative weights of P and M cells are β_P and β_M, then we find the weights that minimize

$$\sum_{\text{gain}} (\beta_P S_P + \beta_M S_M - C)^2$$

where C is the observed contrast, and $S_P, S_M \geq 0$ are the power preferred by the P and M cells respectively. As shown below, this optimization is performed both for 1) each individual and 2) for all individual data combined.

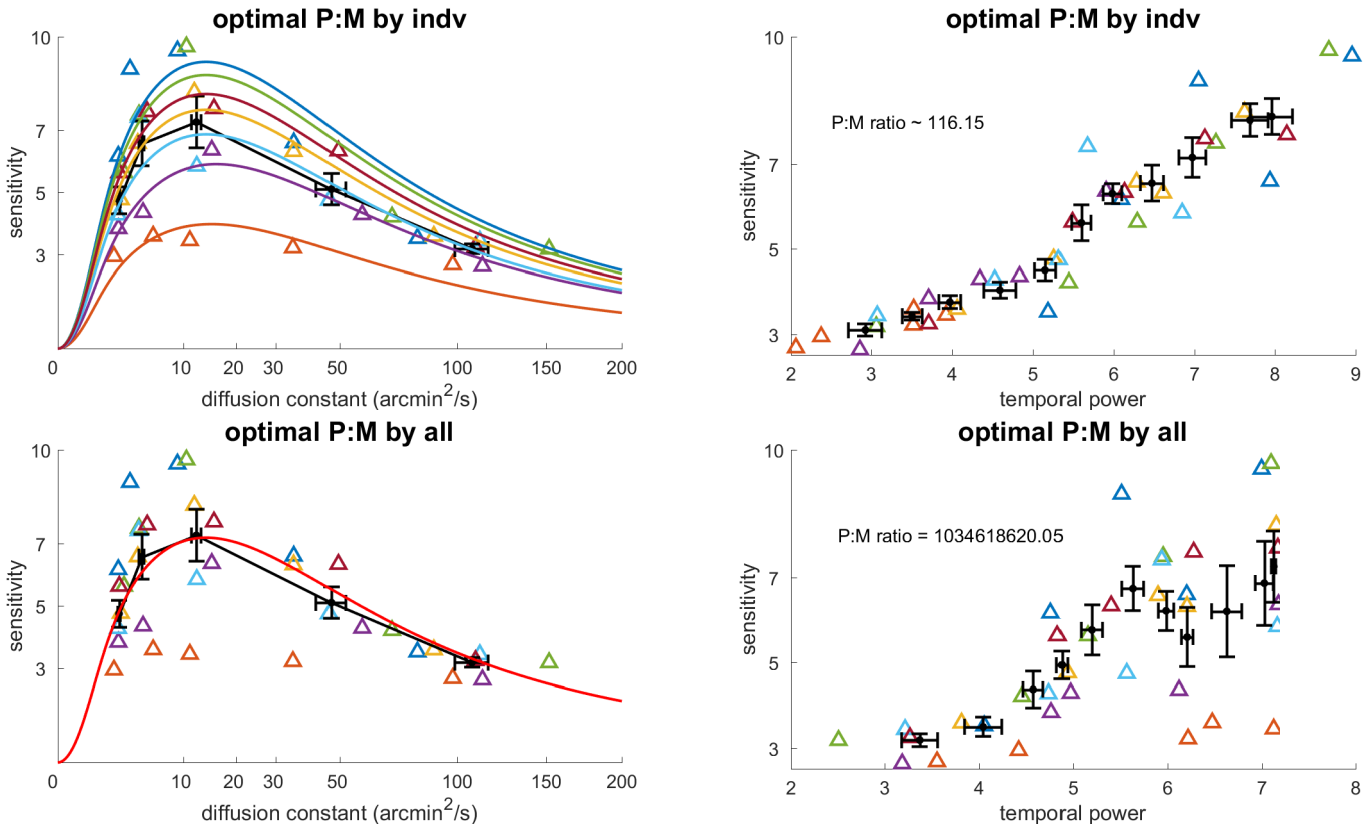
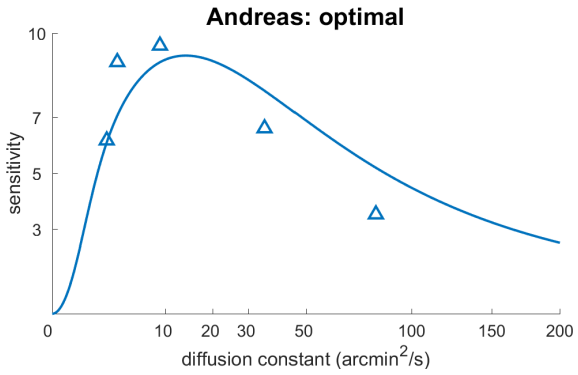
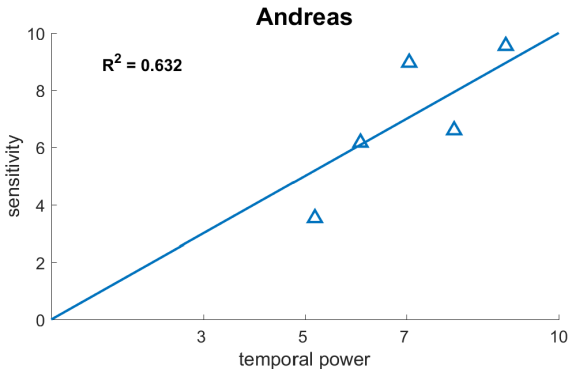
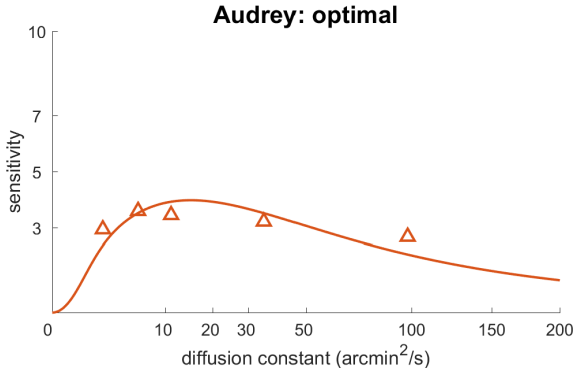


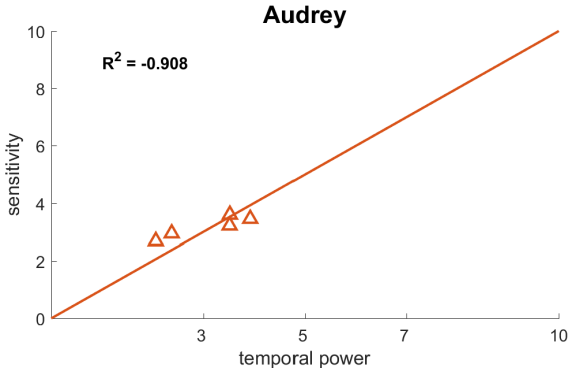
Figure 6: Sensitivity and model vs diffusion constant when the extrafoveal P:M cell ratio is optimized (but basically infinite) and power is integrated over 0.63-80Hz. Parameters are now optimized so that temporal power is on the same scale as sensitivity. TOP: optimization to each individual. BOTTOM: optimization to all data points together.

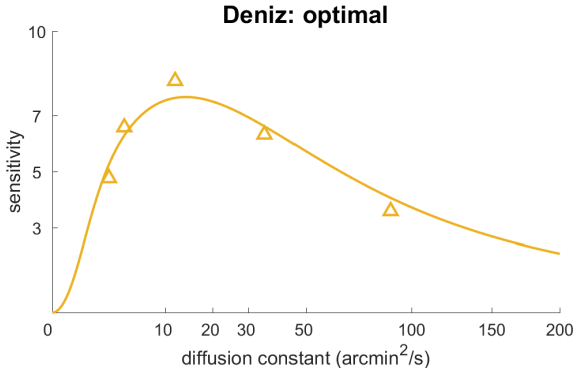
3.3 Individual fits - optimal ratio by individual

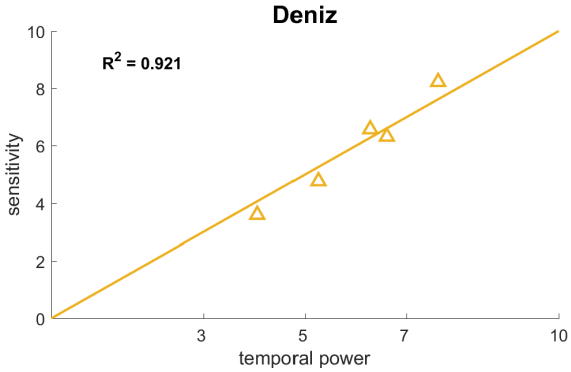


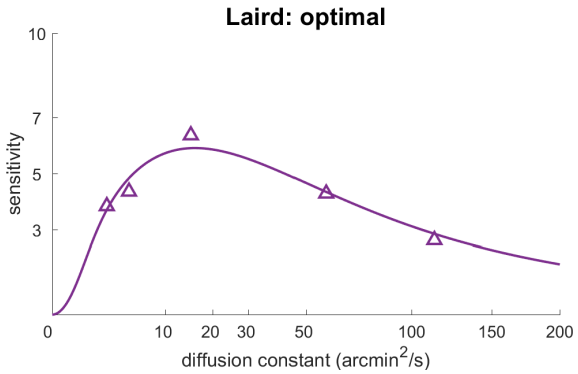


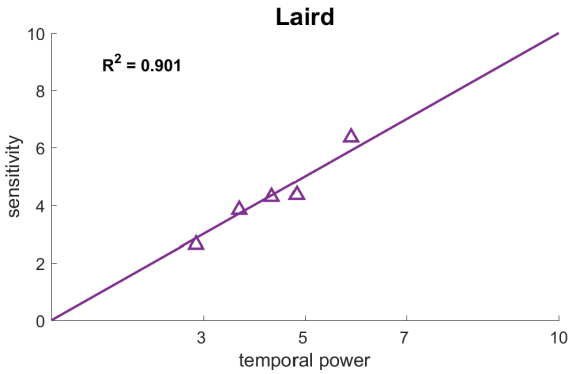


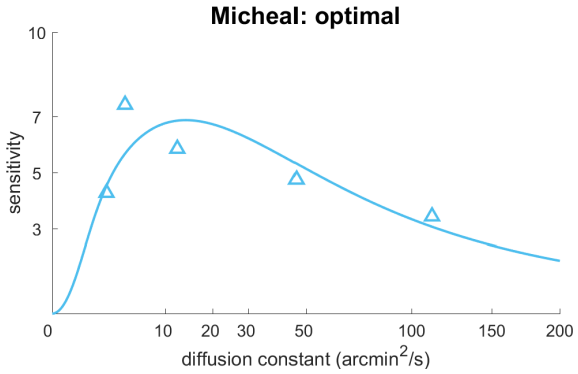


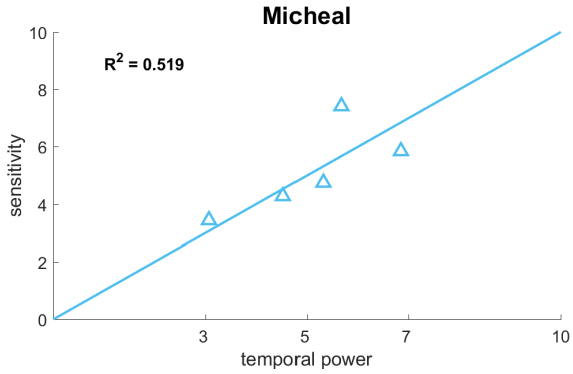


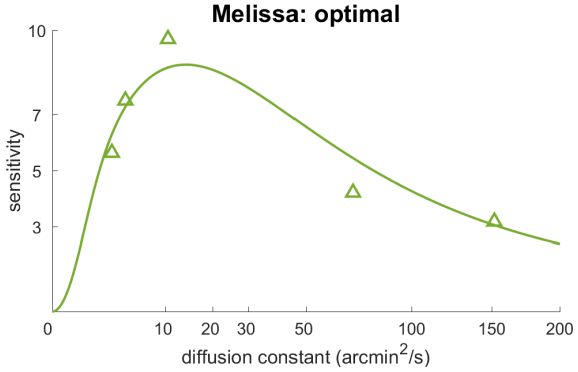


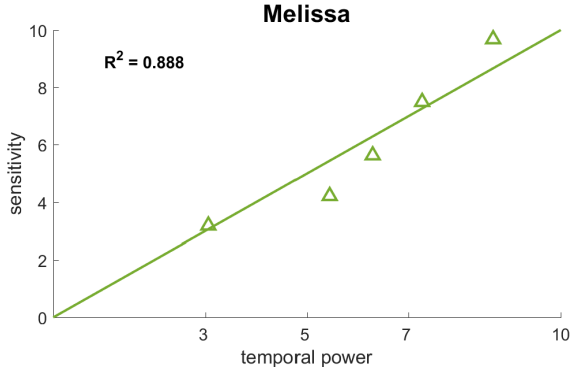


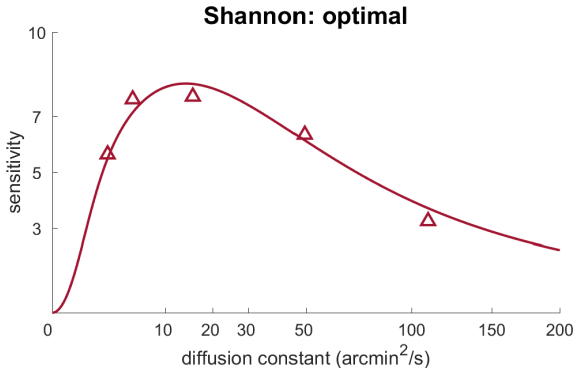


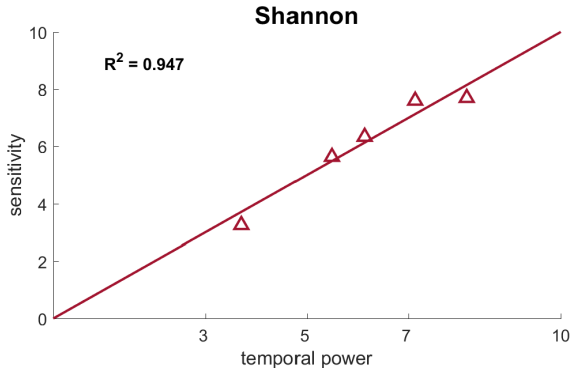

Micheal: optimal
sensitivity
diffusion constant (arcmin^2/s)


Micheal
R^2 = 0.519
sensitivity
temporal power


Melissa: optimal
sensitivity
diffusion constant (arcmin^2/s)


Melissa
R^2 = 0.888
sensitivity
temporal power


Shannon: optimal
sensitivity
diffusion constant (arcmin^2/s)


Shannon
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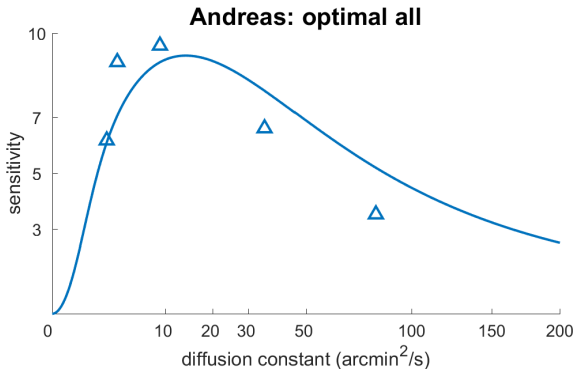
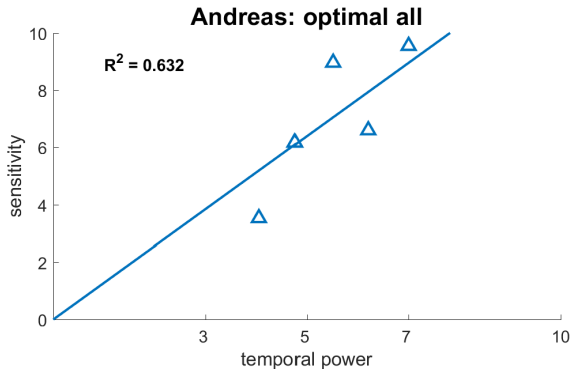
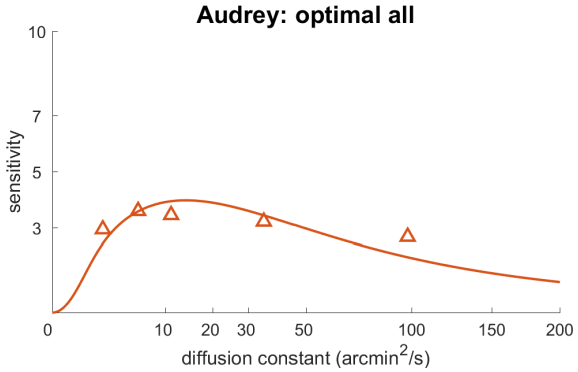
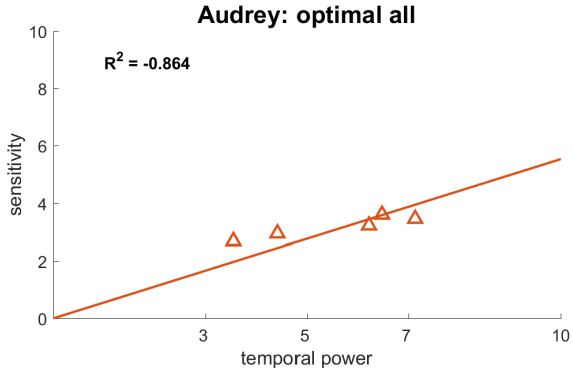
sensitivity
temporal power

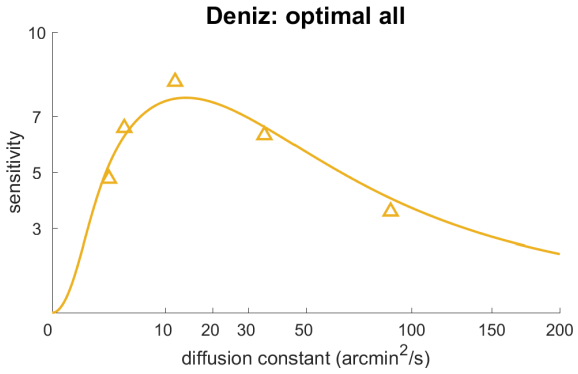
3.4 Individual fits - optimal ratio by all (with additional gain factor)

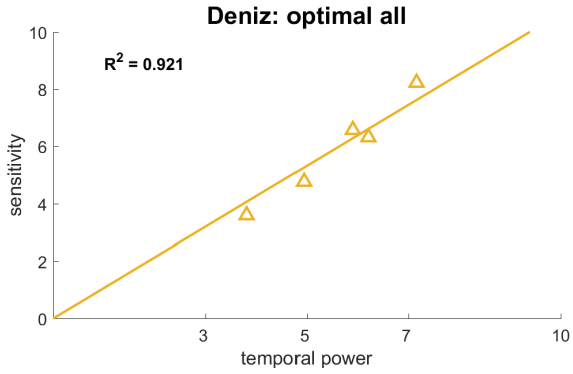


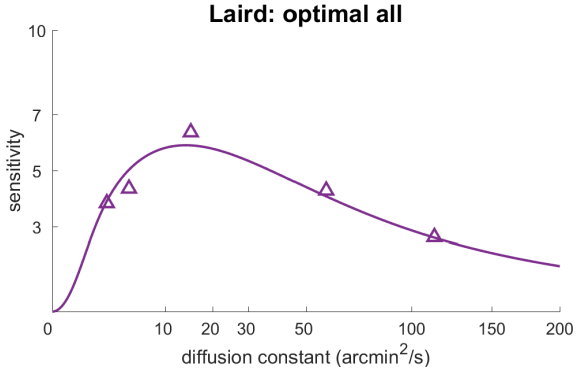


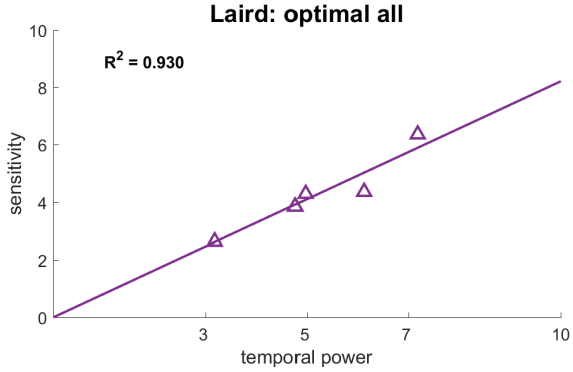


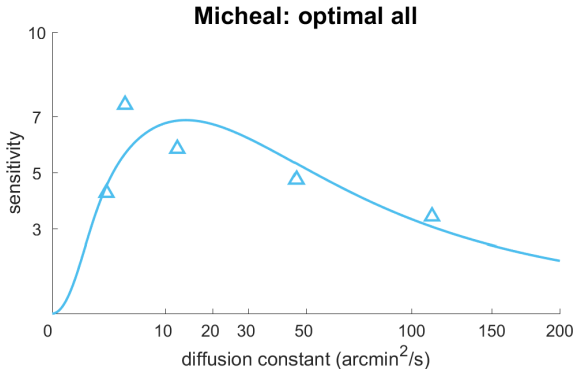


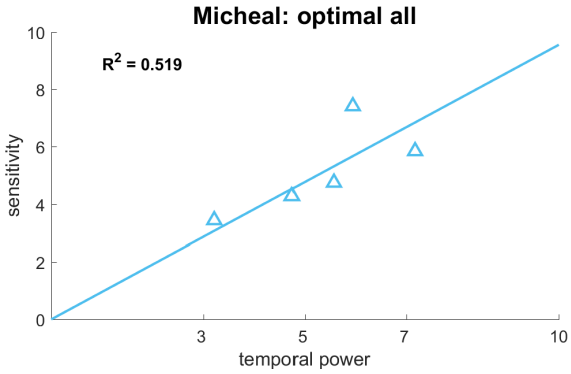


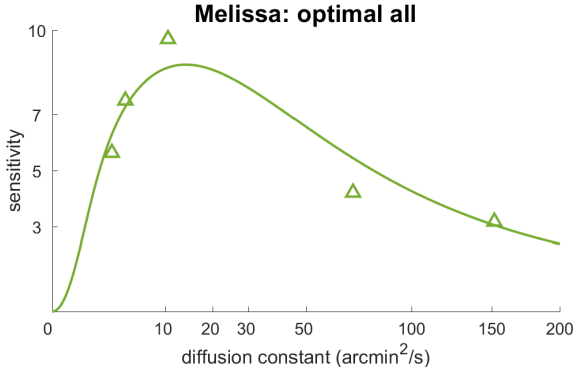


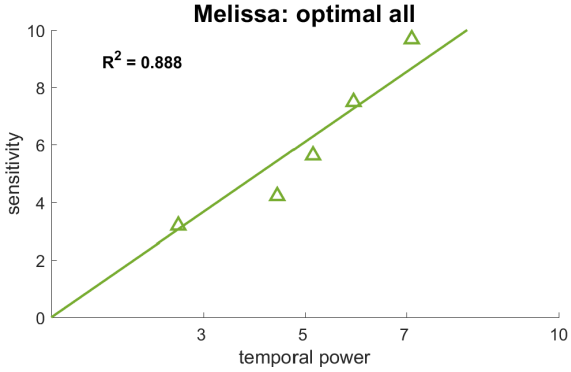


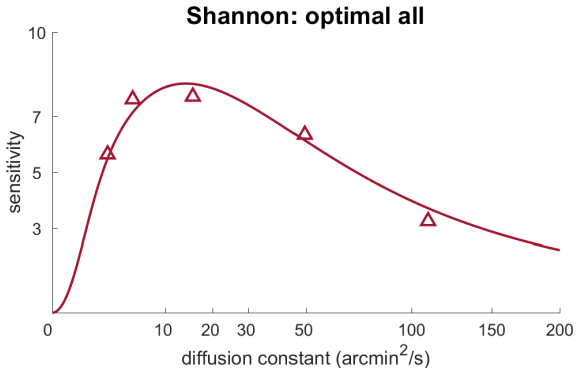


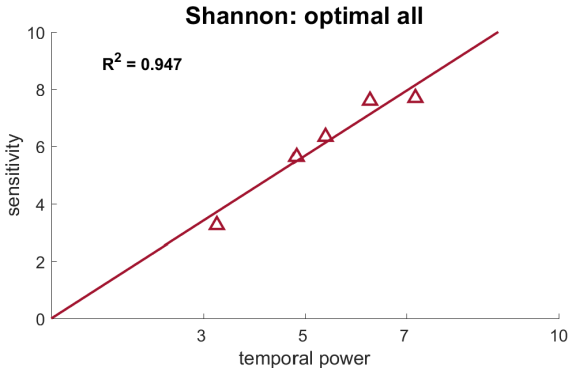

Micheal: optimal all
sensitivity
diffusion constant (arcmin^2/s)


Micheal: optimal all
R^2 = 0.519
sensitivity
temporal power


Melissa: optimal all
sensitivity
diffusion constant (arcmin^2/s)


Melissa: optimal all
R^2 = 0.888
sensitivity
temporal power


Shannon: optimal all
sensitivity
diffusion constant (arcmin^2/s)


Shannon: optimal all
R^2 = 0.947
sensitivity
temporal power

3.5 P-cell only

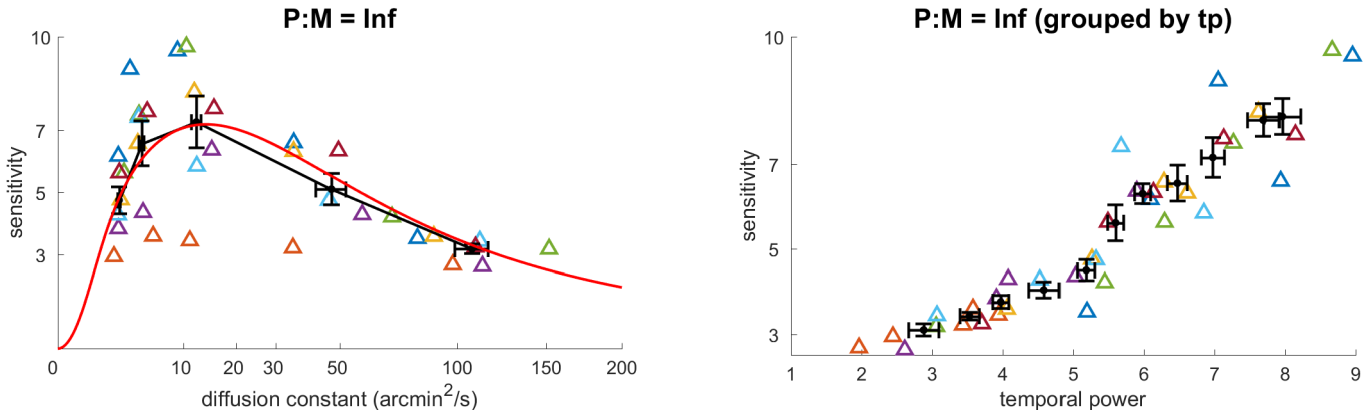
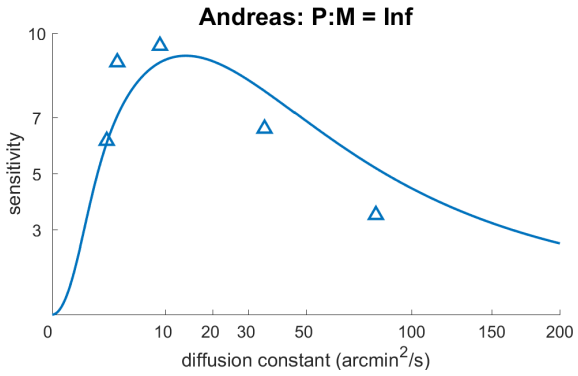
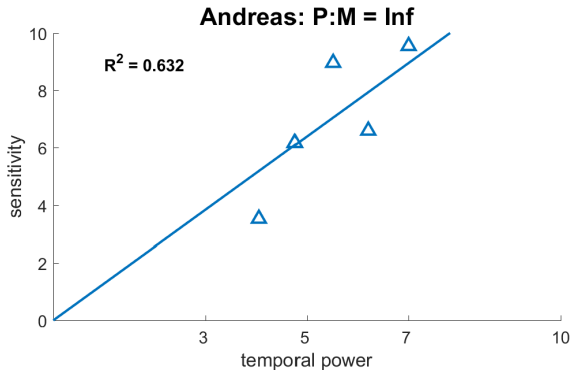
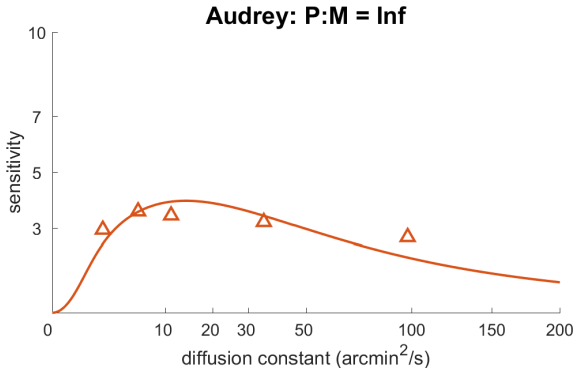


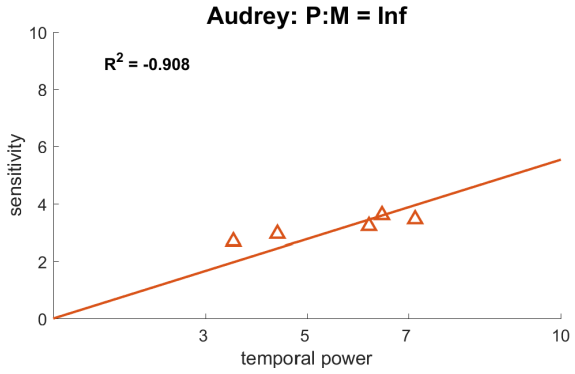
Figure 7: Sensitivity and temporal power vs diffusion constant when only the temporal sensitivity of P-cells is taken into account and power is integrated over 0.63-80Hz. Here the temporal power (RIGHT) is computed with a scaling factor for each individual to normalize across subjects.

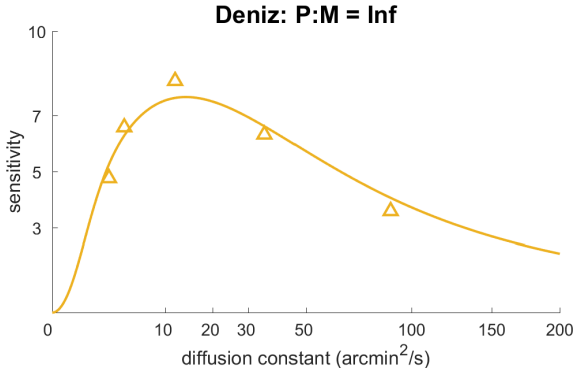
3.6 Individual Fits

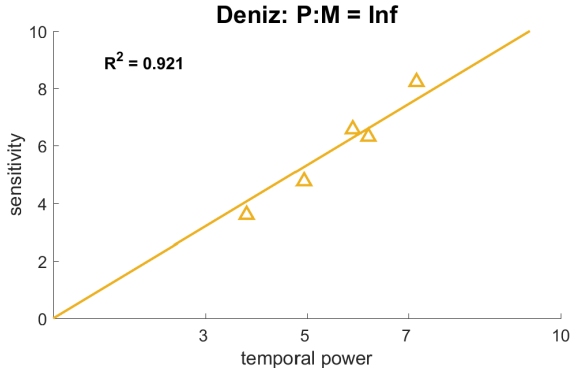


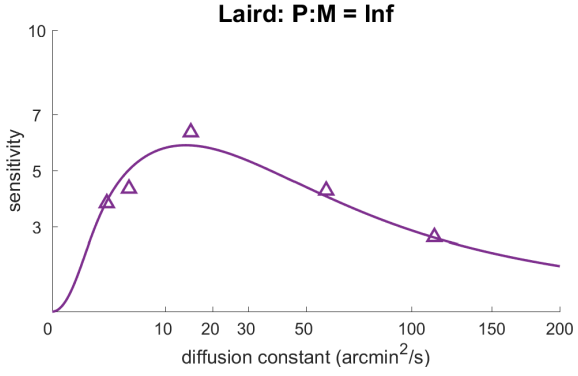


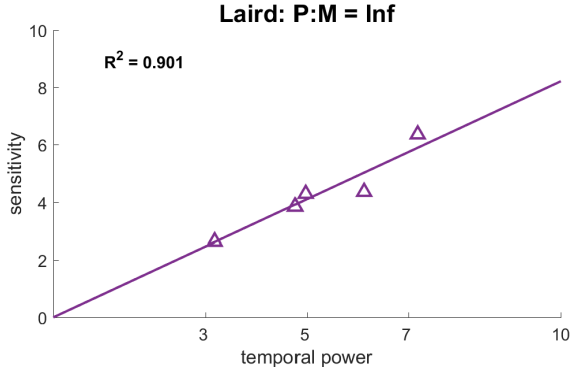


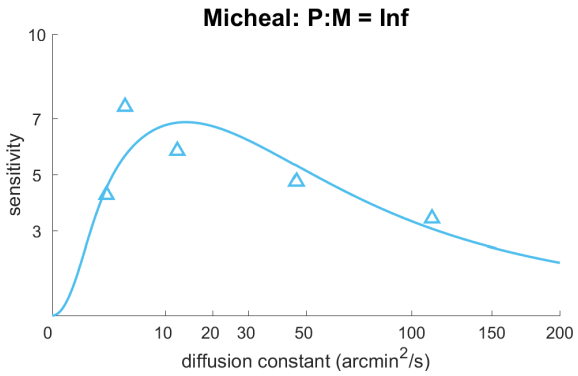


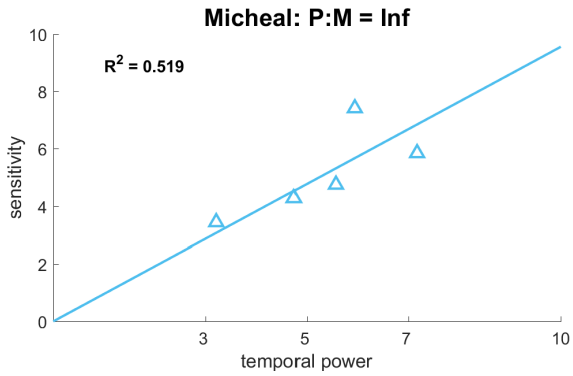


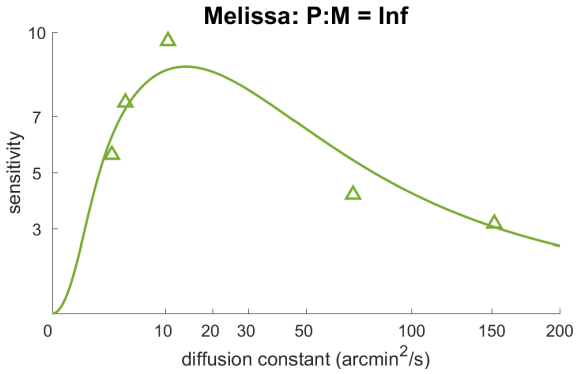


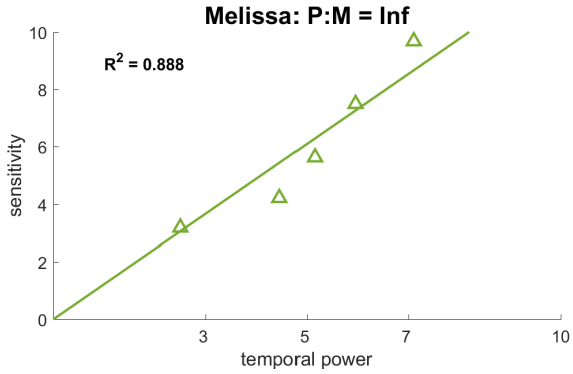


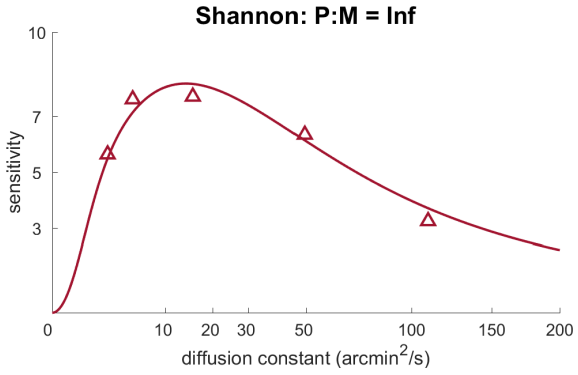


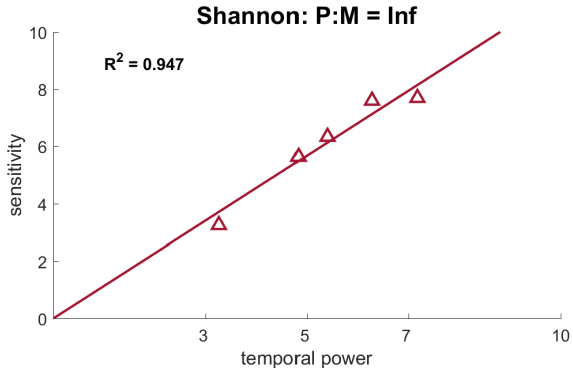

Micheal: P:M = Inf
sensitivity
diffusion constant (arcmin2/s)


Micheal: P:M = Inf
R2 = 0.519
sensitivity
temporal power


Melissa: P:M = Inf
sensitivity
diffusion constant (arcmin2/s)


Melissa: P:M = Inf
R2 = 0.888
sensitivity
temporal power


Shannon: P:M = Inf
sensitivity
diffusion constant (arcmin2/s)


Shannon: P:M = Inf
R2 = 0.947
sensitivity
temporal power

4 Model Update 2: more accurate P-cell sensitivity

$$S(k=16;D_E) = \int_{f_0}^{100} Q(k=16,f;D_E)H(f)\,df$$

where $H(F)$ is some weighted ratio of H_P and H_M, the temporal sensitivities of P and M cells respectively (fig 8).

The major update in this section pertains to the P-cell profile at low temporal frequencies: Sensitivity under 2Hz is determined by linearly interpolating between sensitivity at 2Hz as predicted by Benardete and Kaplan (1999) and 0 sensitivity at 0Hz (consistent with decrease in sensitivity shown by Purpura et al 1990).

The temporal profile of the experimental stimulus is now included in the form of the cutoff frequency - for a stimulus presentation time of 1.3 seconds, there are ideally no temporal frequencies less than f_0 =1/1.3 = 0.77Hz present in the stimulus.

These changes are implemented in the linearPrediction_v2.m file (see gitlab project).

Note: Results are qualitatively similar when a cutoff of f_0 =0Hz is used - see folder in images: new_0cutoff.

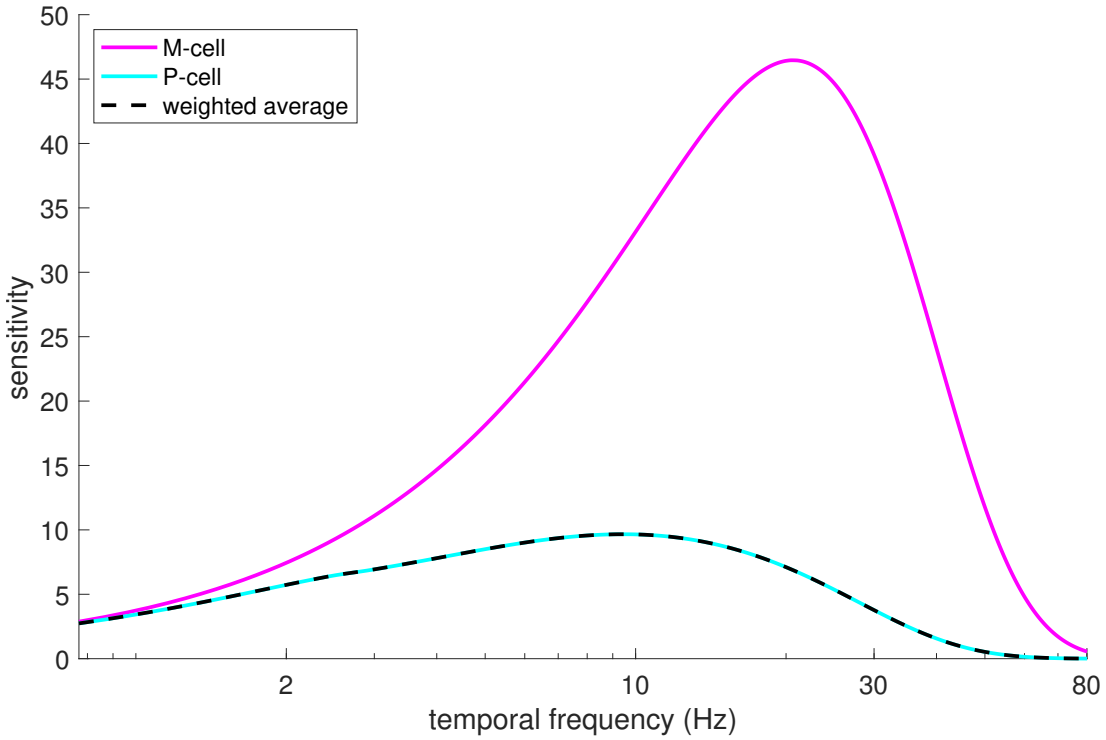


Figure 8: Sensitivity of retinal cells and their average when weighted with an infinite P:M cell ratio. The average sensitivity (black) is used in this updated model (0.77-80Hz).

4.1 Model Update 2: Optimal ratio of P:M cells

(This text is a repeat of above) Here I compute the P:M cell ratio that optimizes the fit between the data and temporal power for both average data and individual data. If the relative weights of P and M cells are β_P and β_M, then we find the weights that minimize

$$\sum_{\text{gain}} (\beta_P S_P + \beta_M S_M - C)^2$$

where C is the observed contrast, and $S_P, S_M \geq 0$ are the power preferred by the P and M cells respectively. As shown below, this optimization is performed both for 1) each individual and 2) for all individual data combined.

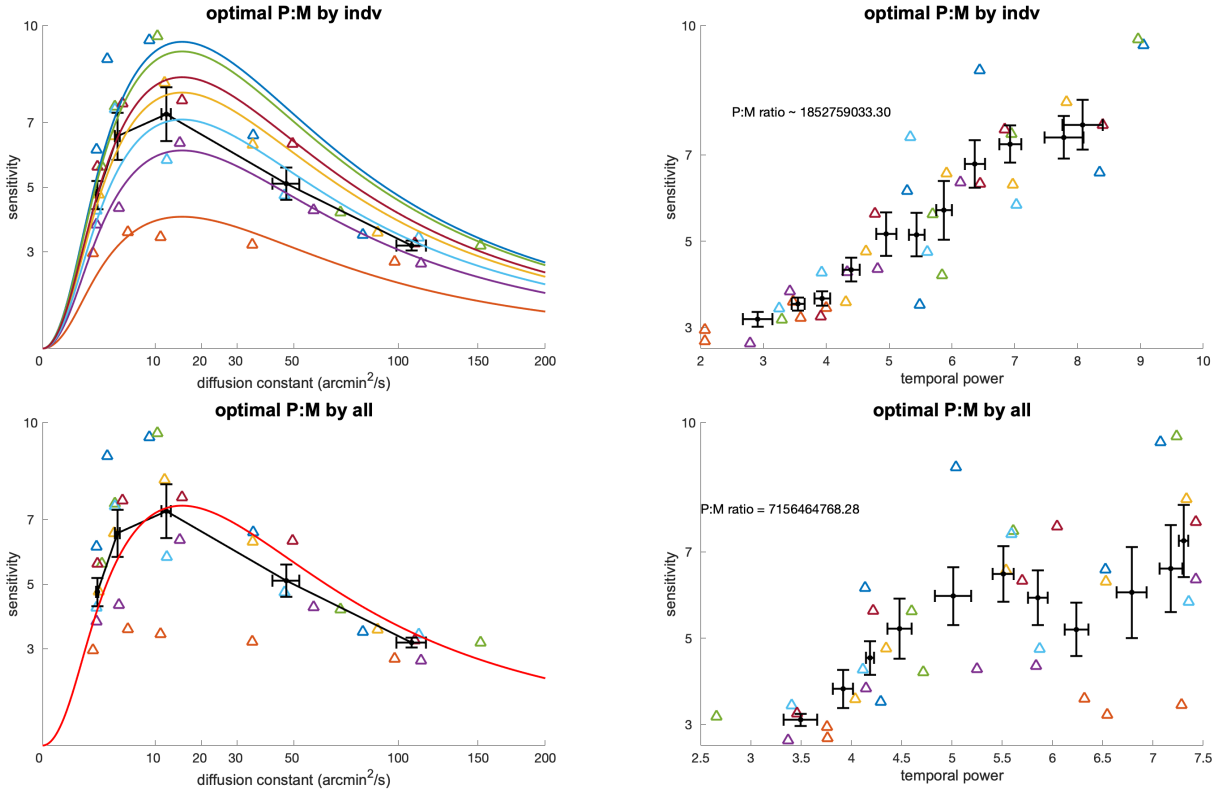
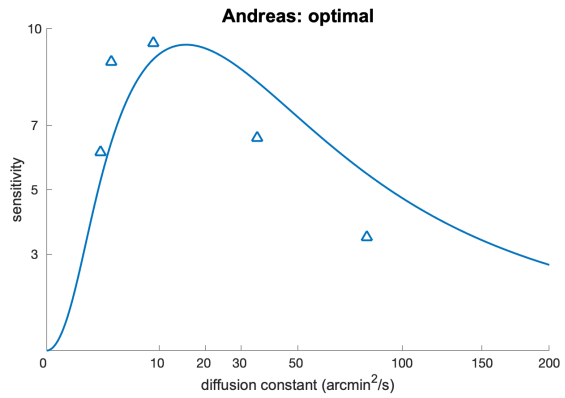
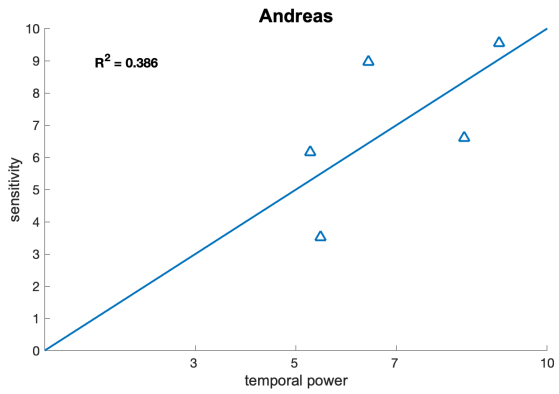
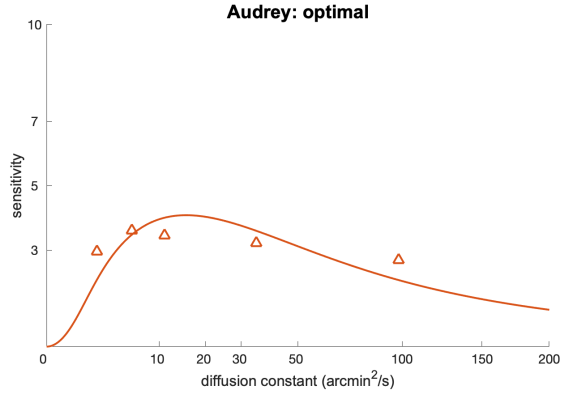


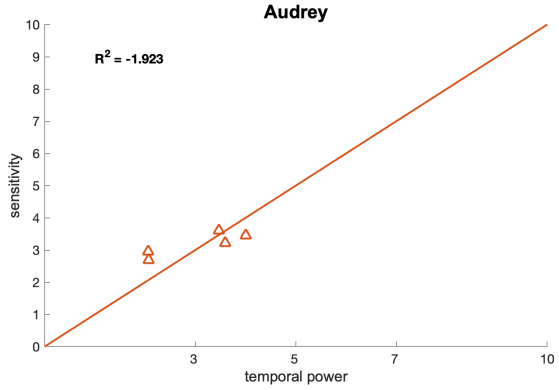
Figure 9: Sensitivity and model vs diffusion constant when the extrafoveal P:M cell ratio is optimized (but basically infinite) and power is integrated over 0.63-80Hz. Parameters are now optimized so that temporal power is on the same scale as sensitivity. TOP: optimization to each individual. BOTTOM: optimization to all data points together.

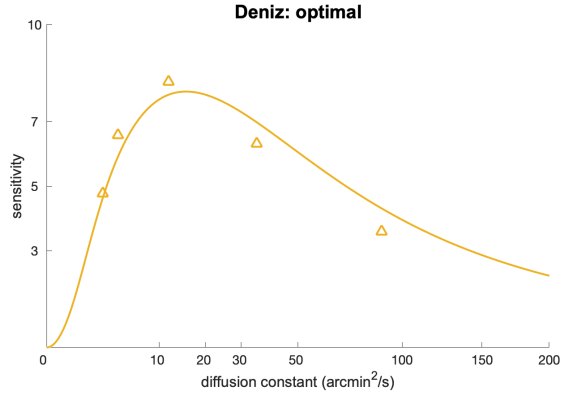
4.2 Individual fits - optimal ratio by individual

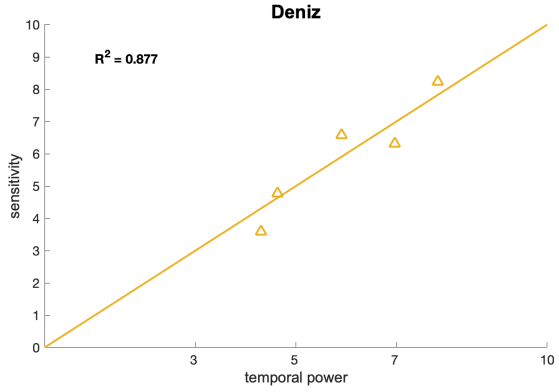


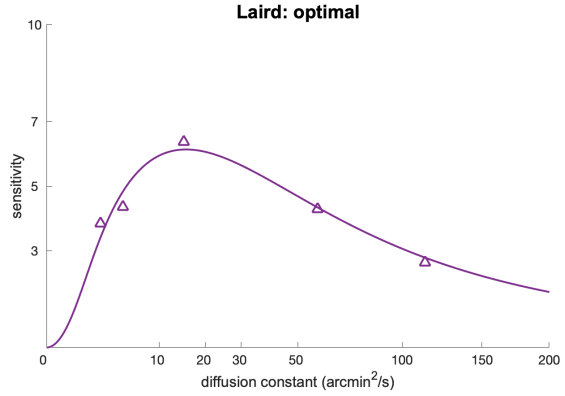


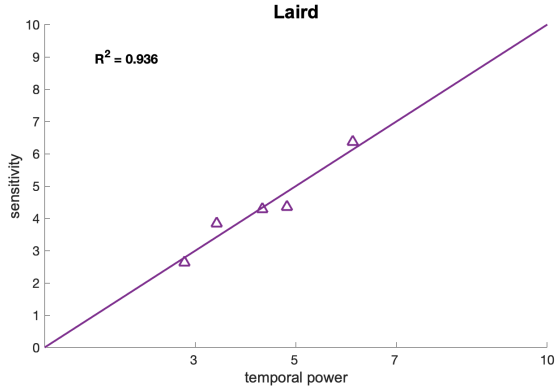


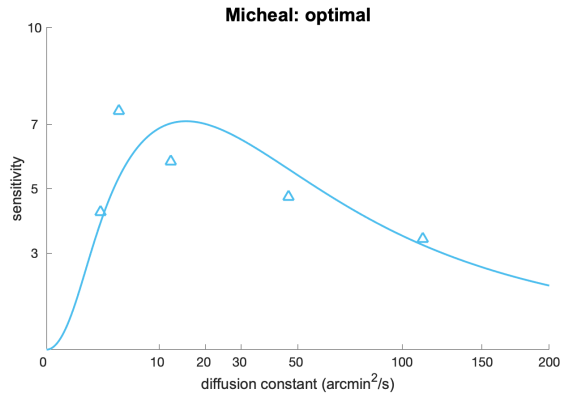


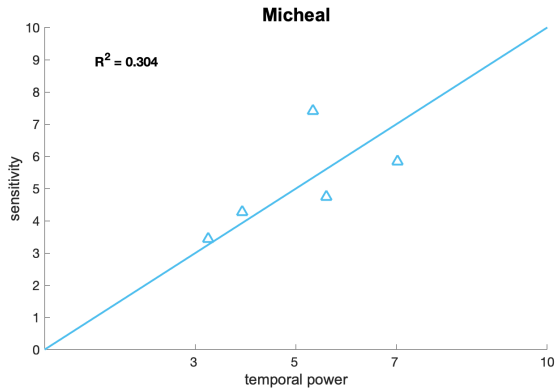


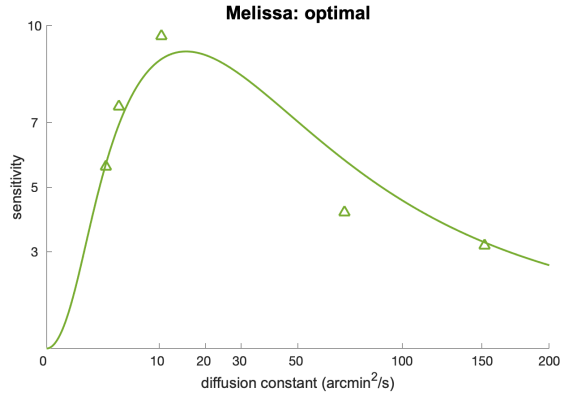


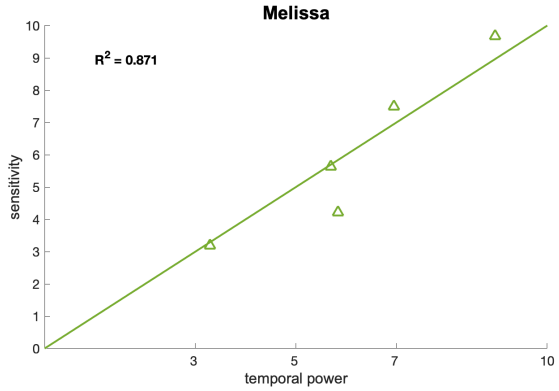


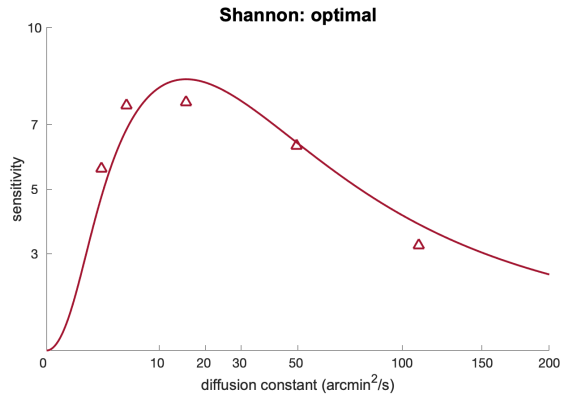


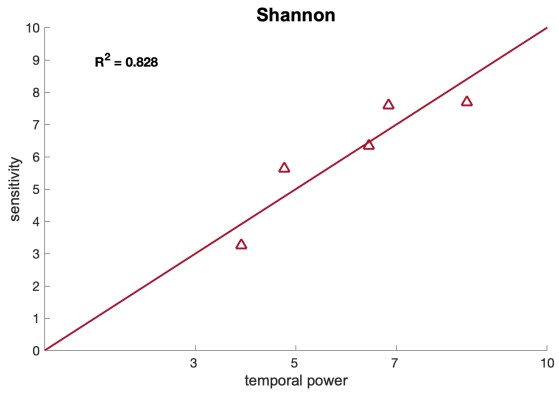

Micheal: optimal
sensitivity
diffusion constant (arcmin^2/s)


Micheal
R^2 = 0.304
sensitivity
temporal power

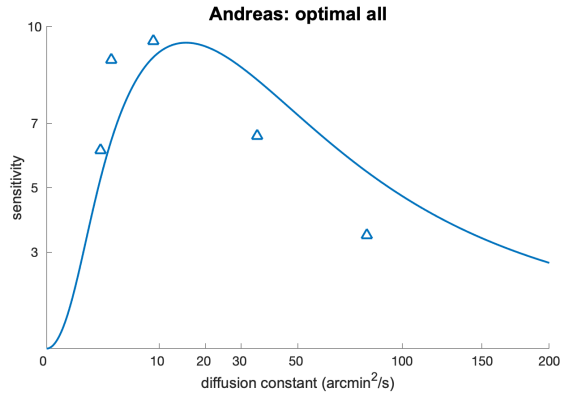

Melissa: optimal
sensitivity
diffusion constant (arcmin^2/s)

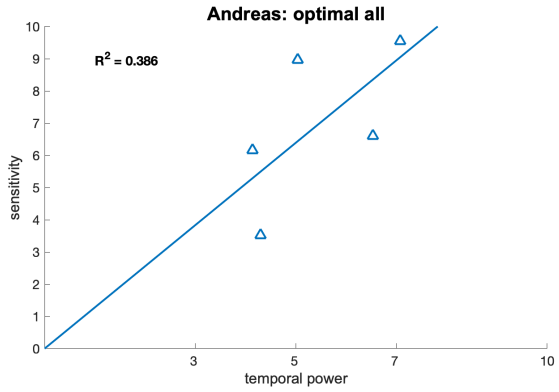

Melissa
R^2 = 0.871
sensitivity
temporal power

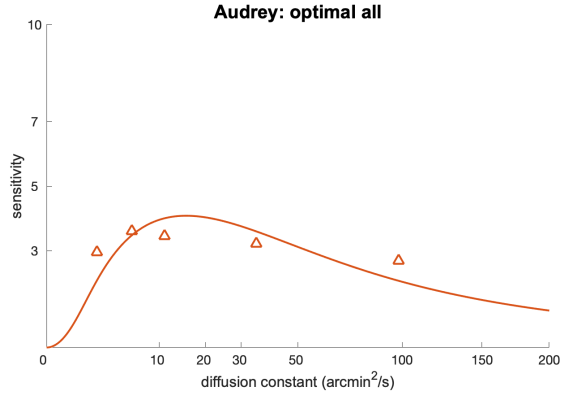

Shannon: optimal
sensitivity
diffusion constant (arcmin^2/s)

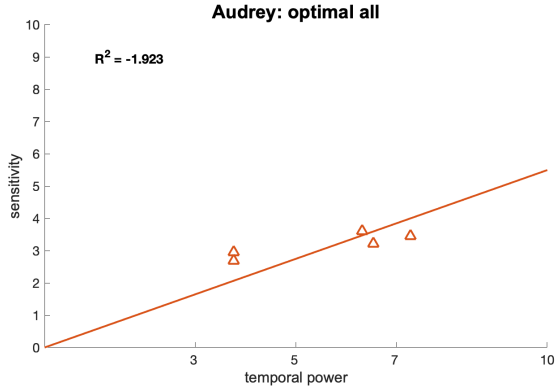

Shannon
R^2 = 0.828
sensitivity
temporal power

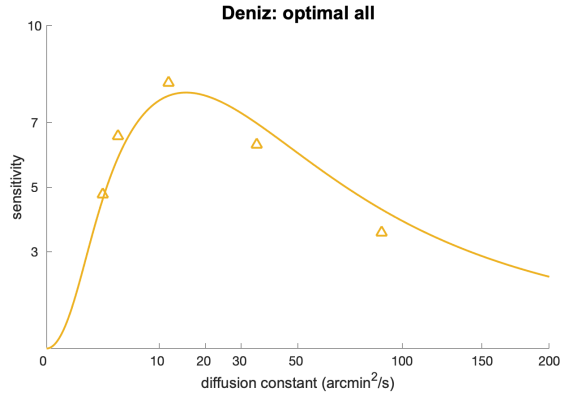
4.3 Individual fits - optimal ratio by all (with additional gain factor)

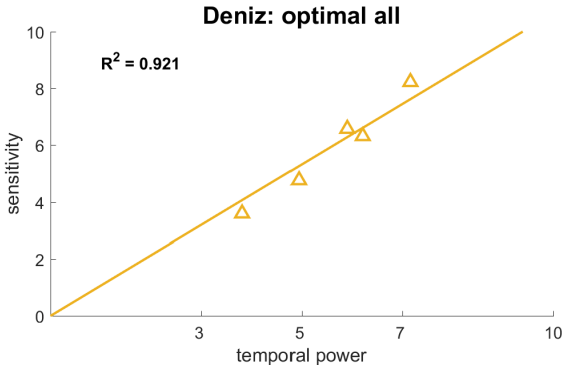


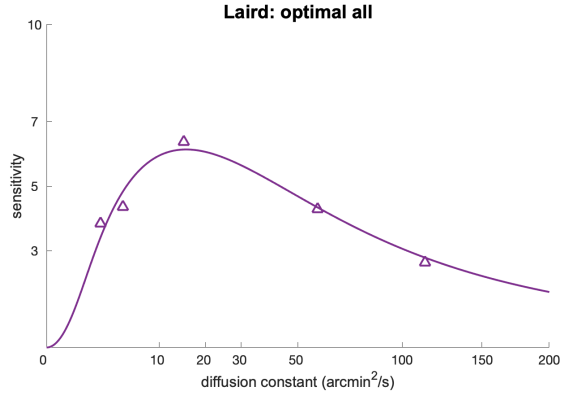


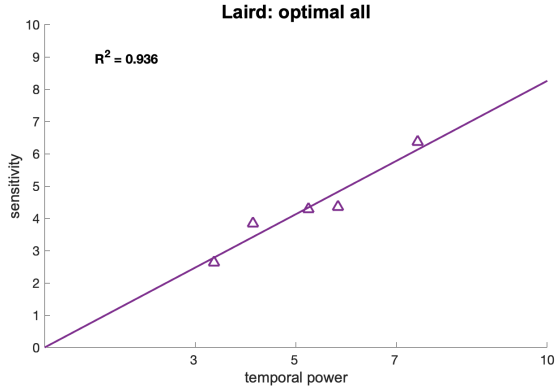


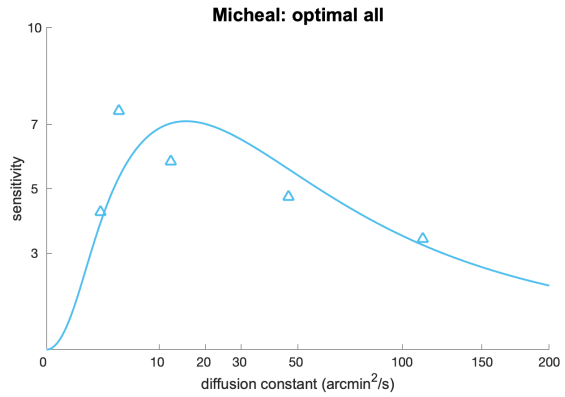


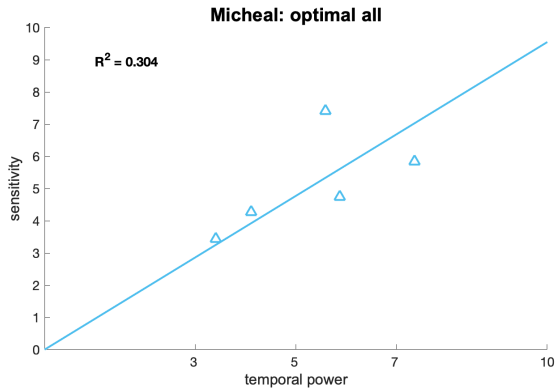


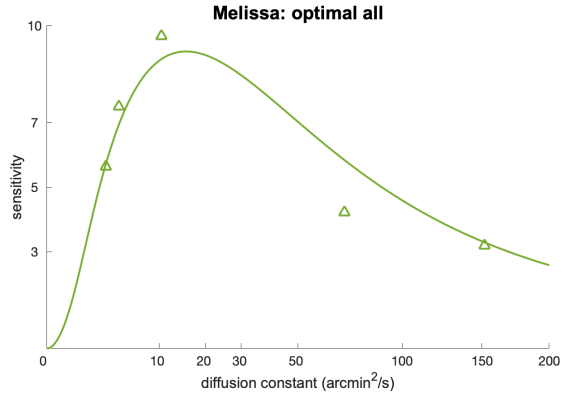


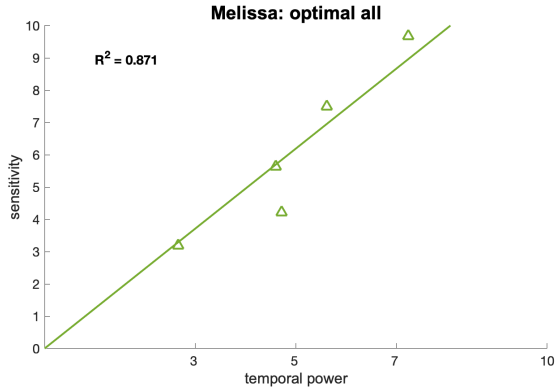


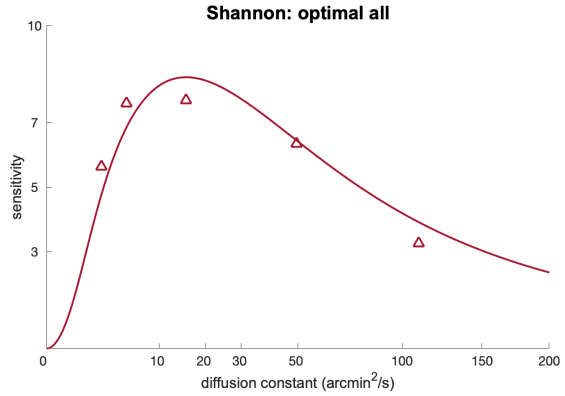


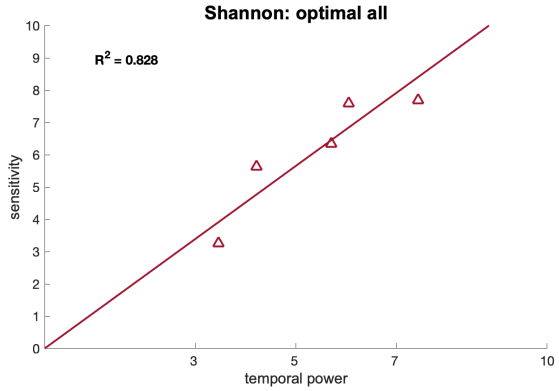

Micheal: optimal all
sensitivity
diffusion constant (arcmin^2/s)


Micheal: optimal all
R^2 = 0.304
sensitivity
temporal power


Melissa: optimal all
sensitivity
diffusion constant (arcmin^2/s)


Melissa: optimal all
R^2 = 0.871
sensitivity
temporal power


Shannon: optimal all
sensitivity
diffusion constant (arcmin^2/s)


Shannon: optimal all
R^2 = 0.828
sensitivity
temporal power

4.4 P-cell only

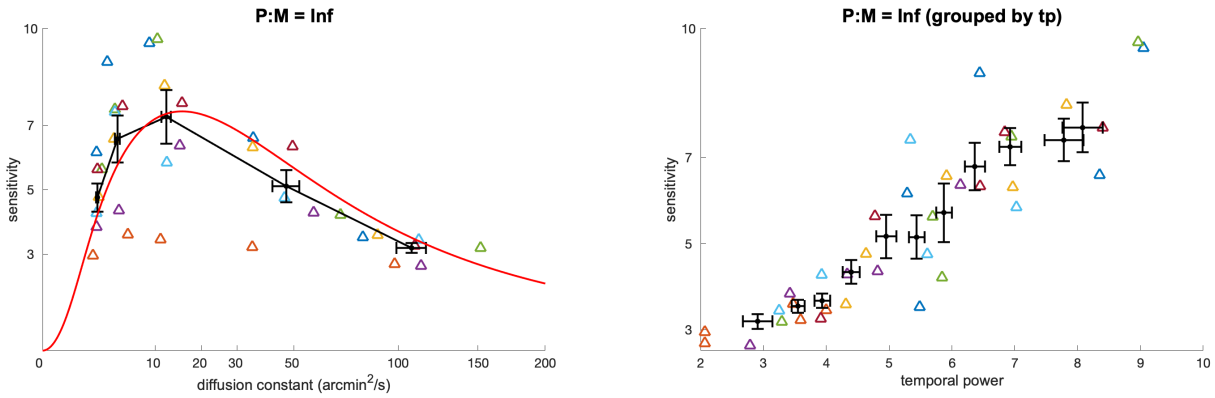
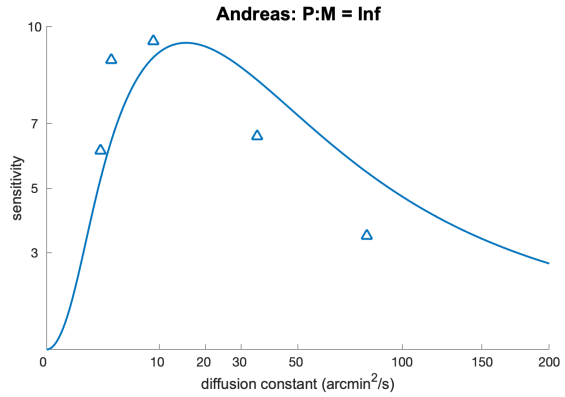
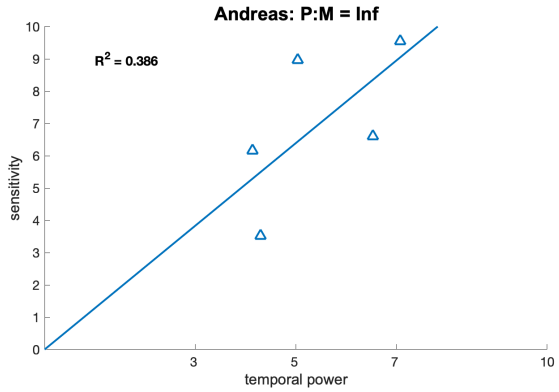
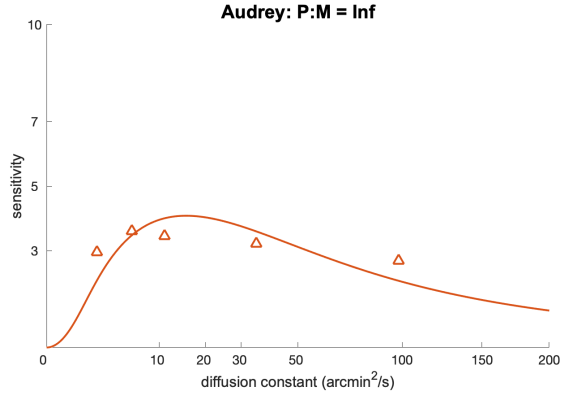


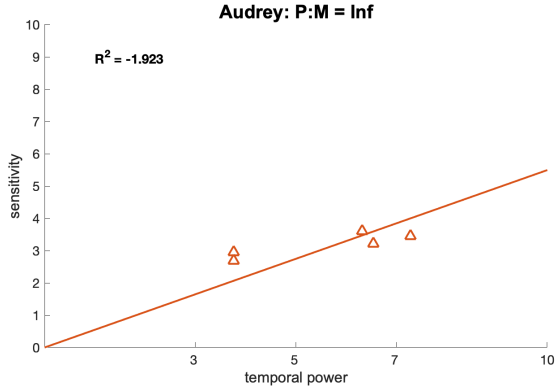
Figure 10: Sensitivity and temporal power vs diffusion constant when only the temporal sensitivity of P-cells is taken into account and power is integrated over 0.63-80Hz. Here the temporal power (RIGHT) is computed with a scaling factor for each individual to normalize across subjects.

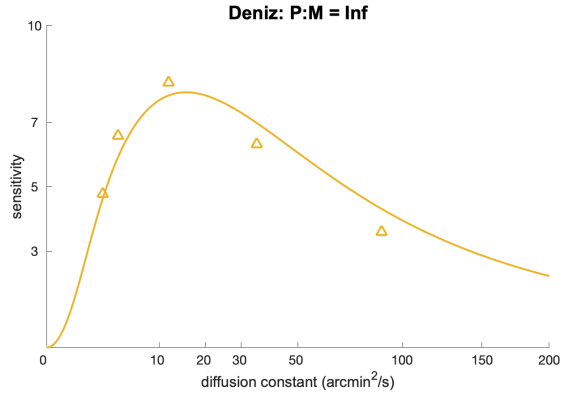
4.5 Individual Fits

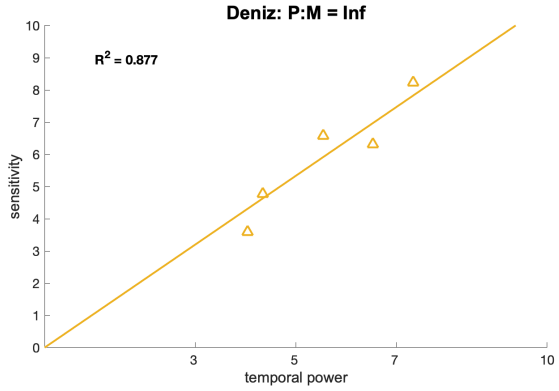


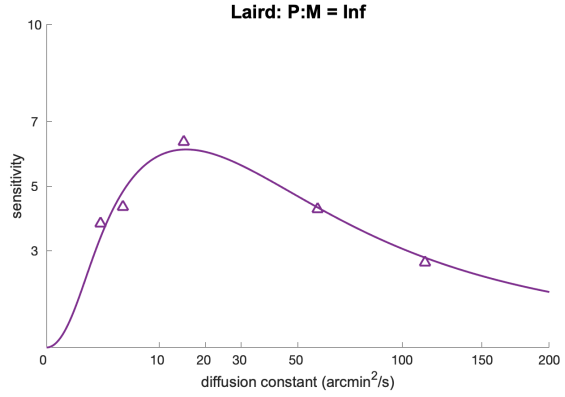


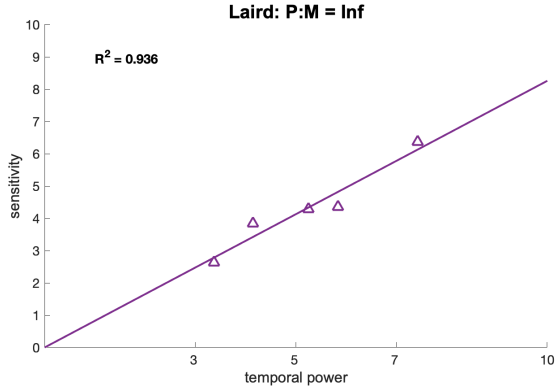


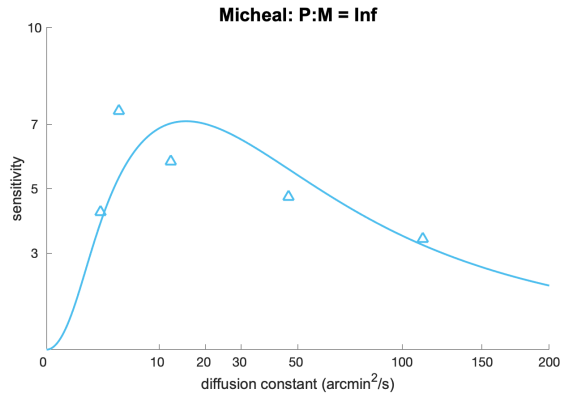


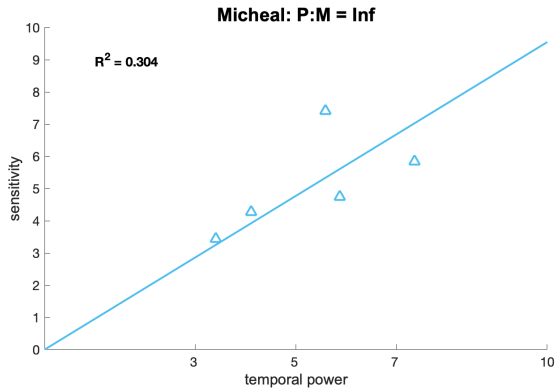


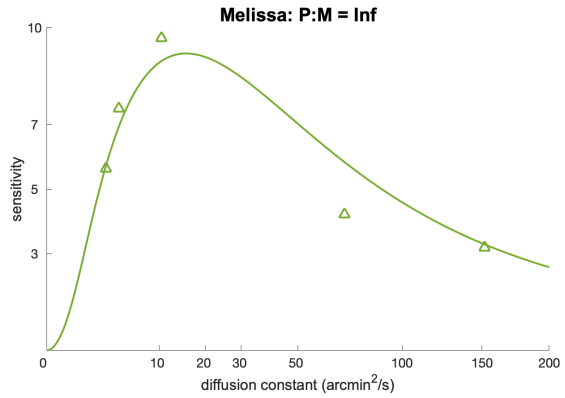


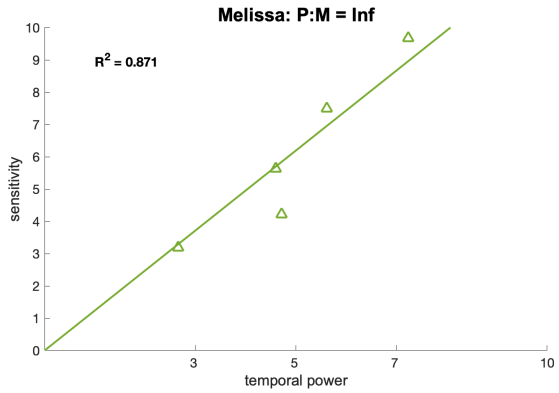


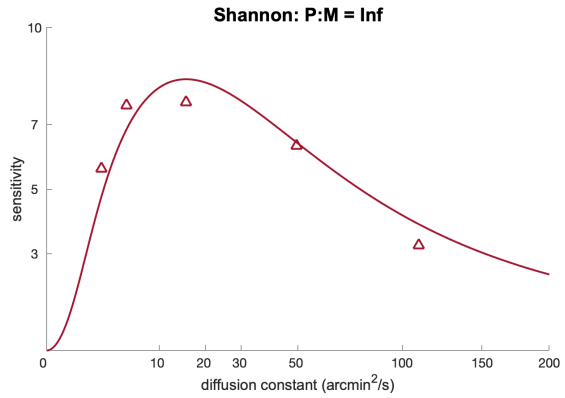


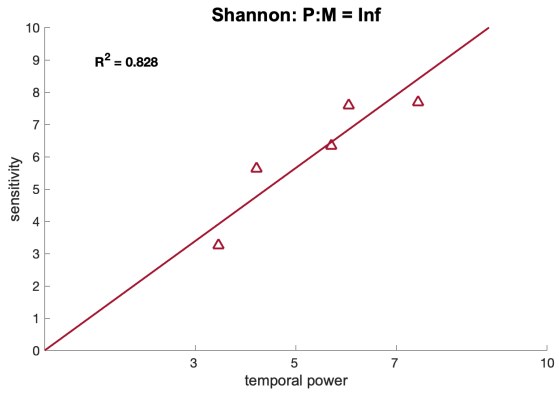

Micheal: P:M = Inf
sensitivity
diffusion constant (arcmin^2/s)


Micheal: P:M = Inf
R^2 = 0.304
sensitivity
temporal power


Melissa: P:M = Inf
sensitivity
diffusion constant (arcmin^2/s)


Melissa: P:M = Inf
R^2 = 0.871
sensitivity
temporal power


Shannon: P:M = Inf
sensitivity
diffusion constant (arcmin^2/s)


Shannon: P:M = Inf
R^2 = 0.828
sensitivity
temporal power