Receptive Fields 2

STRFs, LNPs, and ANNs

Neurophysiology and Behavior, Drew B. Headley, Spring 2021

What we will cover:

A tour of receptive fields (RFs)

- Review of RF definition
- Spectro/spatio temporal receptive fields
- Linear-Nonlinear-Poisson model
- Optimization in neural networks
- Conceptual pitfalls when interpreting RFs

Today we will cover analytical techniques to derive receptive fields.

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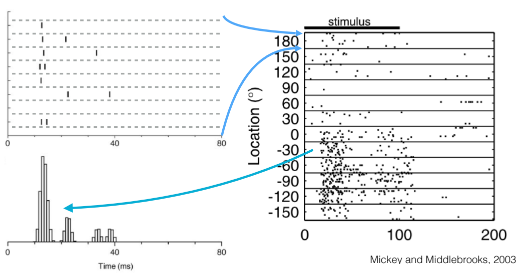
First let's review what we already know about RF construction.

Requirements for defining an RF

- **To construct:**
  - An input, physical modality
  - An output, neuronal signal
  - A way to define similarity between inputs or map them
- **To interpret:**
  - Mapping between input and output must be ‘systematic’
- **To build upon:**
  - Relationship to perception
  - Combinatorial/hierarchical/multiplexed

Same slide as the first lecture.
The first lecture was concerned mostly with the topics in blue.
This lecture is concerned with the topics in red. There are many ways to interrogate the mapping between inputs and outputs. We will discuss the classical approach, followed by a few more advanced ones.

Traditional approach to RF construction



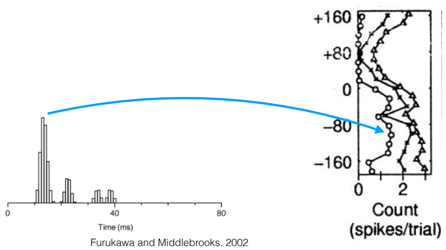
Furukawa and Middlebrooks, 2002

Mickey and Middlebrooks, 2003

The traditional approach is to present a variety of stimuli spanning some stimulus dimensions that should be encoded. Each stimulus is presented multiple times. Often the particular stimuli are chosen randomly on each trial, so that the same stimulus is not repeated several times in a row and potentially habituates the neural response. Once all the stimuli have been presented the neural responses are grouped based on the stimulus. If the response is spiking activity, it is binned into a peristimulus time histogram (PSTH). If the response is continuous, such as in calcium imaging, the mean change in fluorescence is averaged at each time point.

The example here is from two papers examining the localization of sounds, so the stimulus dimension was the azimuth of the sound (horizontal angle).

Traditional approach to RF construction



Furukawa and Middlebrooks. 2002

The peak of the PSTH is measured for each stimulus and plotted along the stimulus axis investigated.
For the case of the plot on the right, this was done for three different sound levels, so three different RFs were generated.

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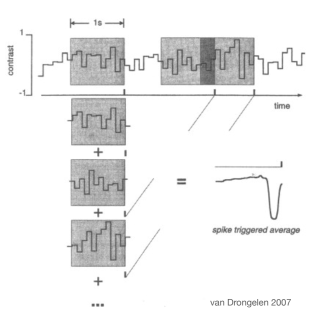
The vast majority of RFs are constructed using the classical approach. But, it has limitations. In particular, the experimenter has to decide what stimulus dimensions matter to the neuron, many stimuli have to be presented to construct the full RF, and one often looses temporal dynamics in the neural response.

One way around this promoted in the early 1970s…

Spike-triggered average

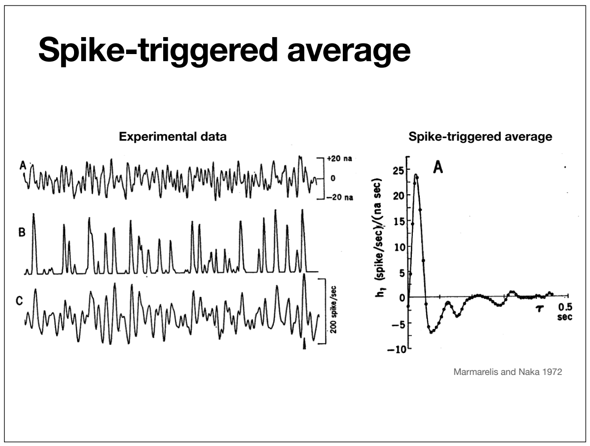


van Drongelen 2007

The idea is to deliver a stimulus that has sufficient complexity to sample many aspects of the stimulus space, and then find the average stimulus that drove spiking. This was known as a spike-triggered average.

In the example shown here, the contrast of a visual stimulus is varied randomly and spiking activity is recorded from a neuron. When the neuron spikes the time course previous 1 sec of the contrast is sampled and stored. Upon completion of the stimulus, these time courses are averaged together, giving the mean dependence of spiking on changes in stimulus contrast.

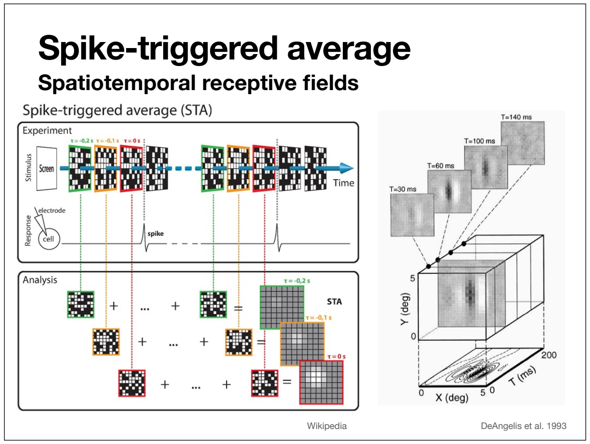
This example is not what we would traditionally consider to be an RF, but it has several advantages and can be generalized to produce RFs.



One distinct advantage is that it allows us to predict the spiking of a neuron given an arbitrary stimulus. The spike-triggered average can be thought of as a filter that describes the relationship between the stimulus and spiking activity (sometimes referred to as a kernel).

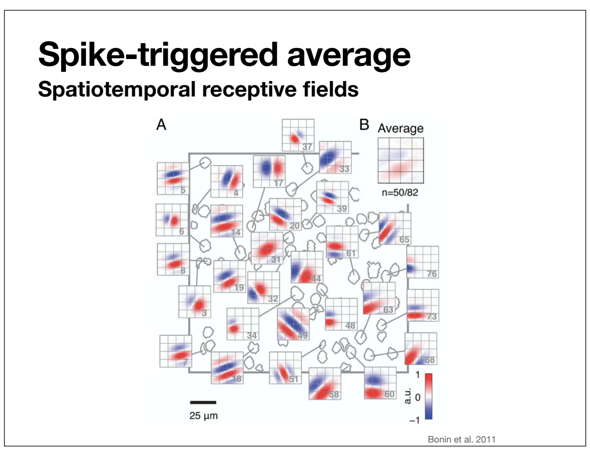
The graph shown here is an early example of this. On the left top the stimulus was a current injected into a neuron that was presynaptic to a retinal ganglion cell. The spiking of the retinal ganglion cell was recorded concurrently (left middle). From these, a spike-triggered average (sometimes referred to as a kernel) was derived. When this convolved with the stimulus, it gave the predicted firing rate of the neuron.

Again, the spike-triggered average is not a proper RF, but it when we infer it using more complex (i.e. multidimensional) stimuli it can be used to generate one.

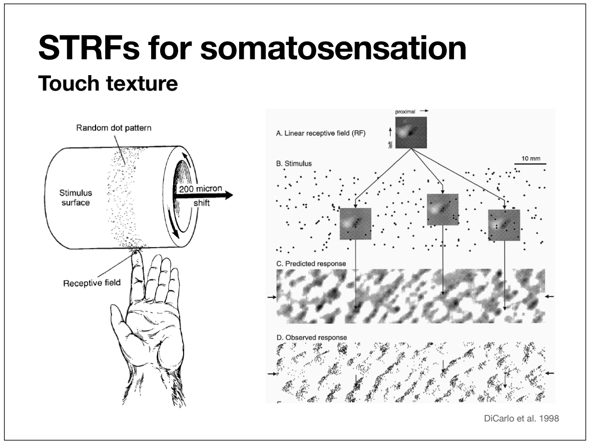


A more complex stimulus could be a random checkerboard of illuminated squares on a screen. These random checkerboard patterns are frequently used to derive receptive fields in the visual system. Using the same spike-triggered averaging approach, now applied to each pixel, we can obtain the spatiotemporal properties of the stimulus that optimally drive a neuron. This will usually have a clear correspondence to a neuron's RF that is derived by the traditional method. These are referred to as STRFs.

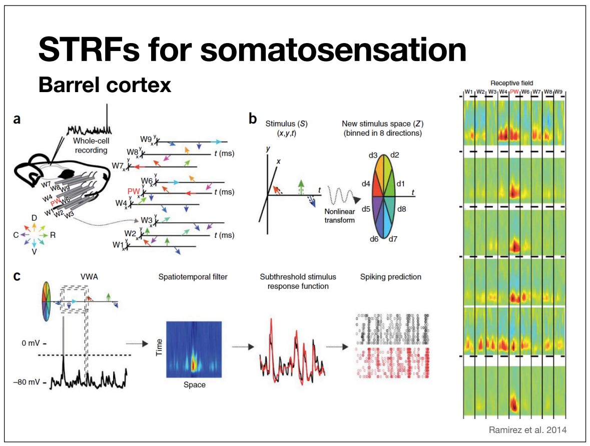
Performing this on retinal ganglion cells often shows retinopic response areas (left), similar to what Hartline described. Not surprisingly, if you do this for neurons in V1 you often see edge or gabor-like kernel (right).



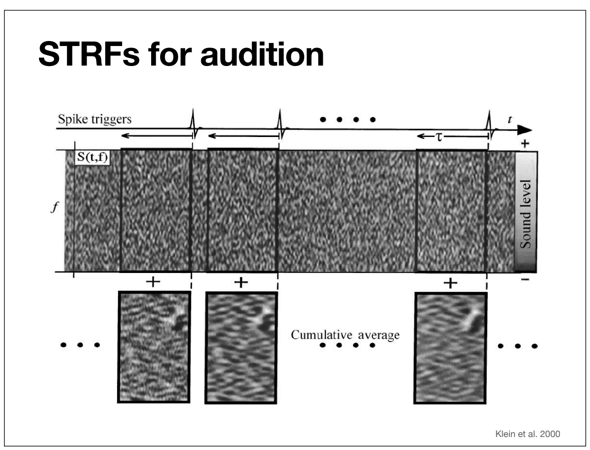
This can also be performed with calcium imaging data, as seen in this example. Importantly, a variety of tuning properties are evident. One can see that orientation, spatial frequency, and retinotopic location were all encoded across the population. Normally one would have to present separate sets of stimuli to probe each of these stimulus dimensions. But, with the random luminance patterned stimuli all dimensions are probed simultaneously.



This technique can be extended to other sensory systems. For instance, to probe the receptive fields associated with surface texture, one can present random dot surfaces to the skin and use the same spike-triggered average calculation.

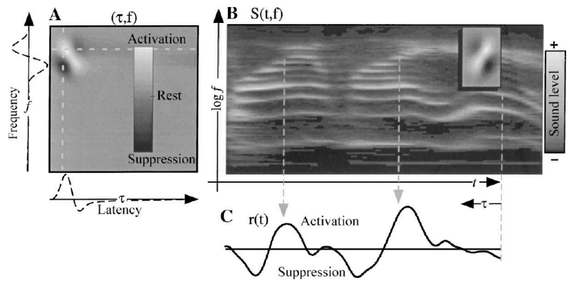


It can also be performed in barrel cortex. In this case, each whisker is independently manipulated towards a random direction (top left schematic). This allows ones to build up a picture of the tuning for neurons in barrel cortex that spans all whiskers and orientations (far right graph).



In the auditory system, the a spike-triggered average can be performed on the spectrogram of a sound. When the stimulus is white noise, all sound frequencies (and their combinations) will be activated eventually. This allows the experimenter to see the neurons spectrotemporal receptive field.

STRFs for audition



Klein et al. 2000

Receptive fields derived using this approach can then be used as filters that are convolved with the spectrogram of other sounds. This allows the experimenter to predict the neuron's response to novel stimuli.

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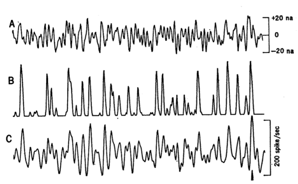
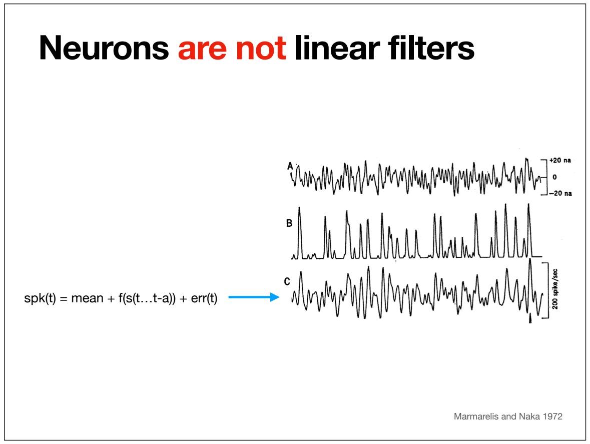
Neurons are not linear filters

- Spiking is a discrete process, either 0 or 1.
- When binned, spikes will be represented as counts, with a minimum value of 0.
- A linear filter dragged across a stimulus will return continuous values and range from positive to negative.

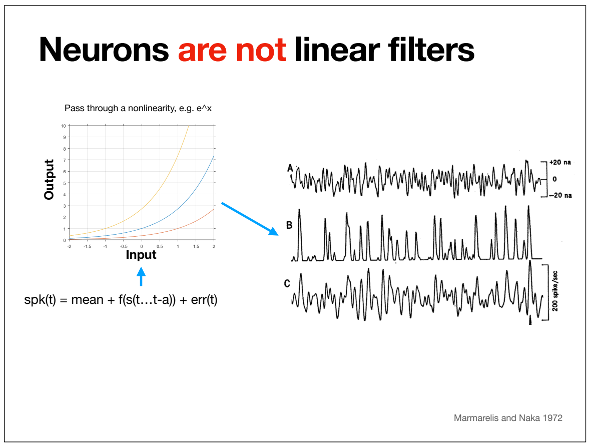


Marmarelis and Naka 1972

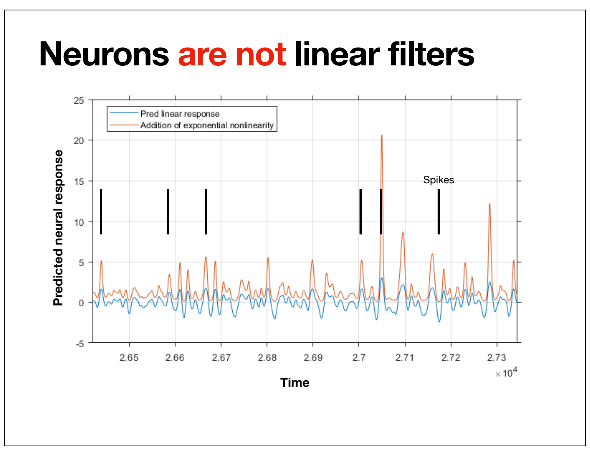
A is the stimulus, B is the observed spiking, and C is the predicted firing from the spike-triggered average.



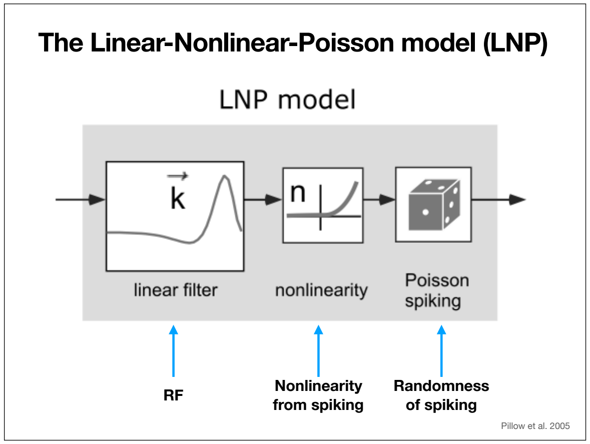
By fitting a linear filter, f, and applying it to the stimulus, s, we can can predict the spiking of a neuron. However, there are problems with this. The predicted spiking in C does not match the observed firing rate in B, for the reasons mentioned in the previous slide.



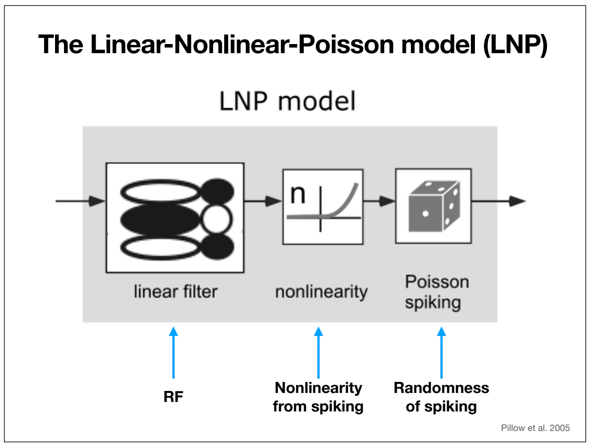
To overcome this, we can apply a nonlinear function, such as an exponential, that forces the predicted spiking to have the properties we know to be the case for real spiking.



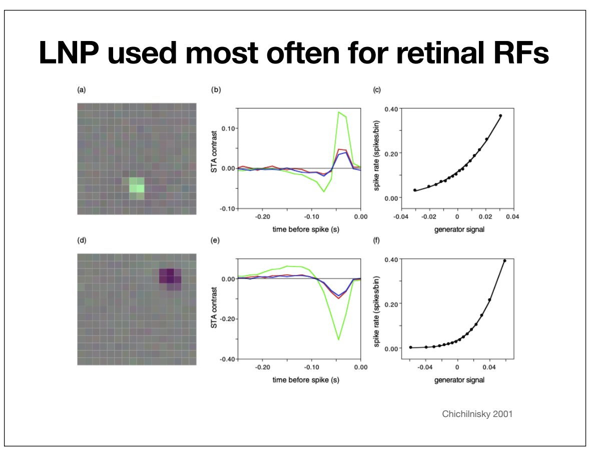
As you can see in this simulated data, the predicted linear response (blue), that once was giving negative firing rates, now only gives positive firing rates (orange). Moreover, the increases in firing have a more pronounced increase, which is in line with observed spiking.
With this predicted firing rate, we can simulate the spiking process itself by passing the rate to a poisson random number generator, which simulates the stochastic nature of spiking (black lines).



This is the LNP model.

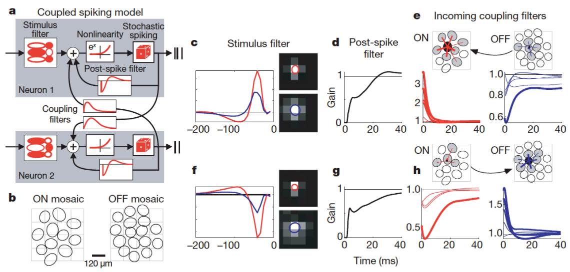


It can be generalized to a wide variety of filters.



It has been used most to understand coding in the retina, with researchers uncovering the spatial restriction of receptive fields and their ON or OFF sensitivity to changes in light level (a,b), their temporal dependence on the change in light level (b,e), and the nonlinear transfer function that gates spiking (c,f).

LNP can scale up to more complex models



Pillow et al. 2008

Most importantly, the model can be scaled up to more complex cases. In this example, the firing of nearby units was added as an additional factor, which captures connectivity between nearby neurons (referred to here as a coupling filter). In addition, the refractory period of the neuron can also be accounted for, using what is called a post-spike filter.

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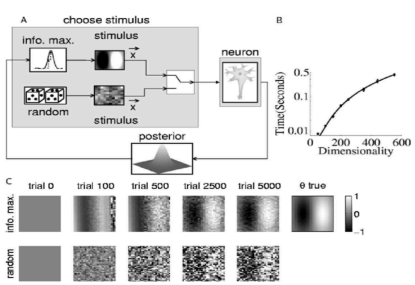
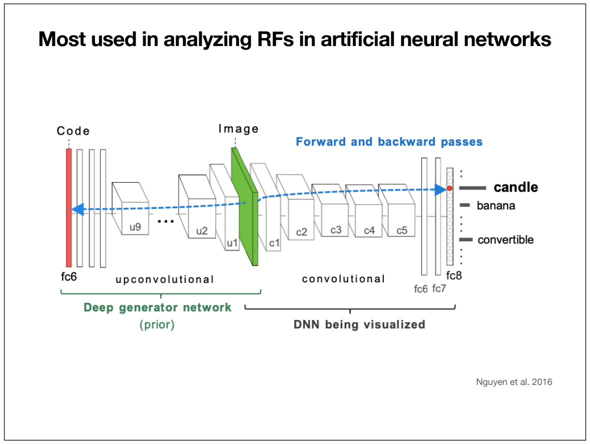
Finding the optimal stimulus

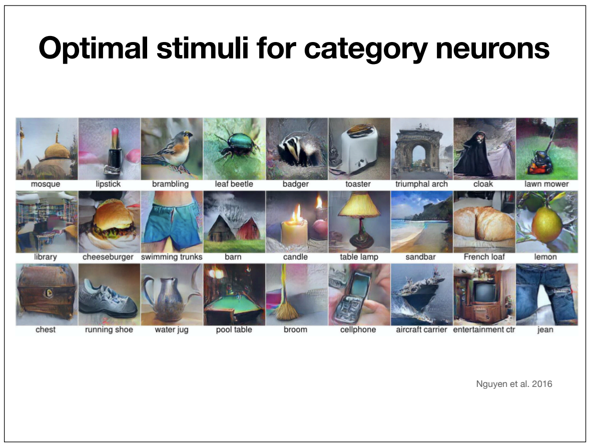


Pillow et al. 2008

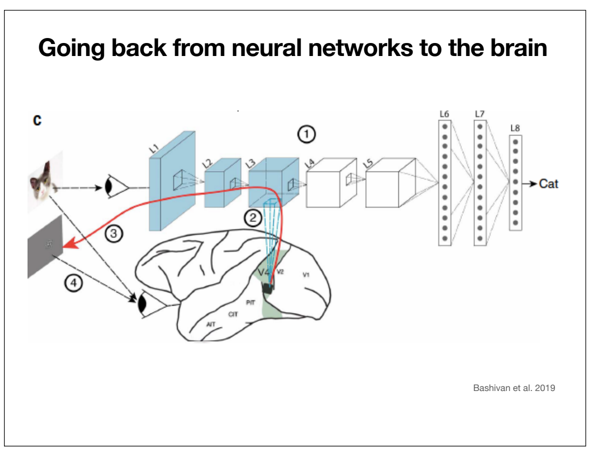
So far we have covered methods to derive receptive fields that entail presenting a series of predefined stimuli. However, it is also possible to start with a random stimulus and optimize it to generate the most spiking. This optimal stimulus often corresponds to the receptive field of the neuron.



That approach is not commonly used in experimental neuroscience, but it has found wide use in determining receptive fields in artificial neural networks. The approach here is to choose a particular unit you want to maximize its response for (in this case the ‘candle’ unit), by optimizing the image (green layer) you pass to the network. The image you generate has a large dimensionality, so the search problem can be reduced by using a generator network (labeled ‘prior’ here), that helps constrain the problem.

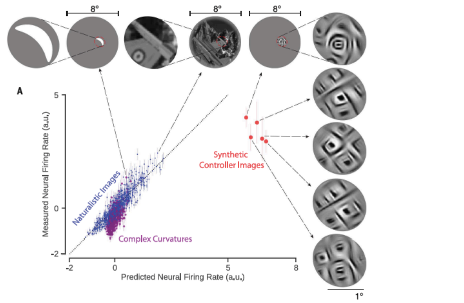


Here are the optimal stimuli for category selective neurons using this approach.



Neural networks can also be used to interrogate receptive fields in the brain. In this example a network was trained to categorize a set of images, and the response of units in one of its layers (L3) was found to be similar to neurons in V4 of monkey visual cortex.

Going back from neural networks to the brain



Bashivan et al. 2019

Having established that correspondence, the experimenters were able to find the optimal stimuli that drove neurons in L3, and then see if they also drove neurons in monkey V4 better than the natural stimuli. Indeed, this turned out to be the case (red dots in scatter graph).

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Conceptual pitfalls when interpreting RFs

- How real is the RF?
- Do RFs promote homuncular thinking?
- How does RF plasticity impact our interpretation of their function?
- Do RFs produced by artificial stimuli capture the coding of naturalistic stimuli?

If we have time remaining, here are some discussion points we can go over to close out our discussion.

Assignment

Each of you will be assigned a paper. You have to identify the technique used to construct the receptive field, and then explain how one of the other approaches we discussed in this lecture could have been used instead.