# Formation of Direction Selectivity in Natural Scene Environments

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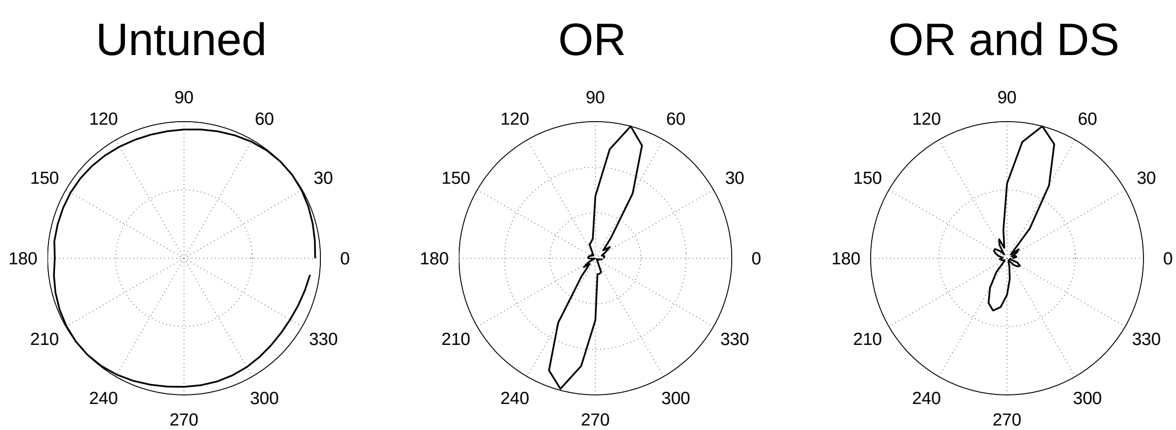
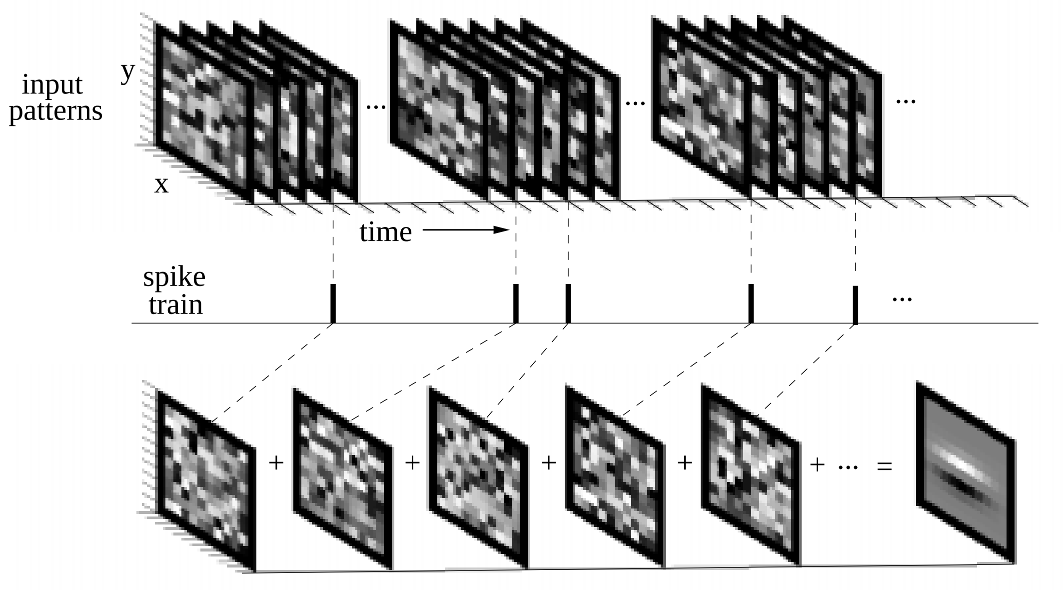
# DIRECTION SELECTIVITY

- most simple cells are orientation selective (OR) and direction selective (DS)
- direction selective (DS) cells respond stronger to a sine grating moving in one direction than the opposite direction



# REVERSE CORRELATION:

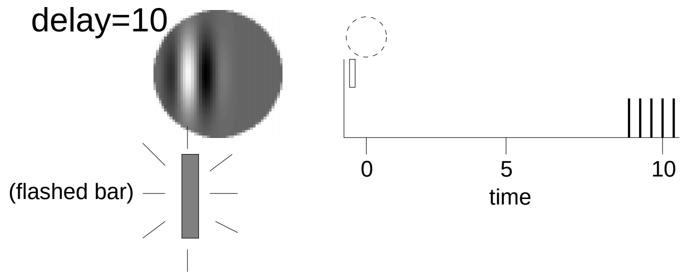
# SPATIOTEMPORAL RECEPTIVE FIELDS



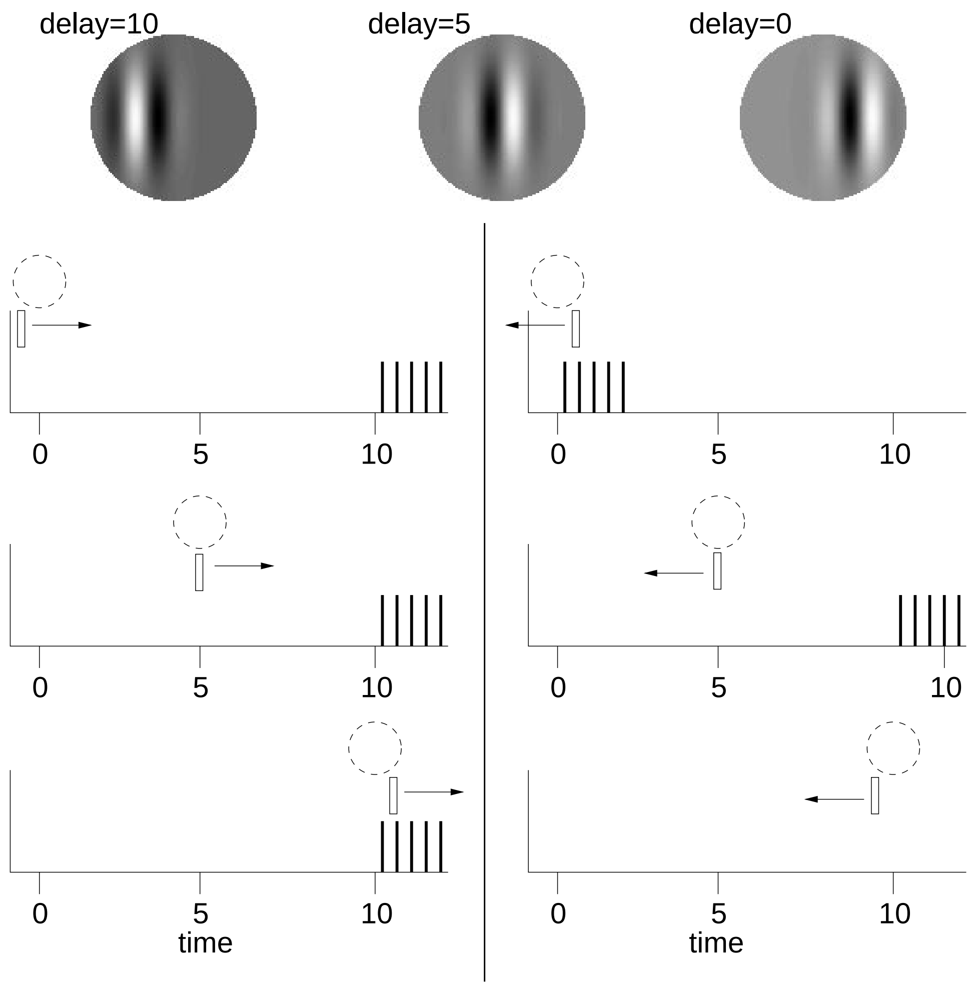

- present random stimulus
- take patterns at a certain delay from each spike
- add patterns to yield RF
- RF is a function of delay
- spatiotemporal receptive field (ST RF) : $K(x, t)$

# How does DS arise from ST RF?

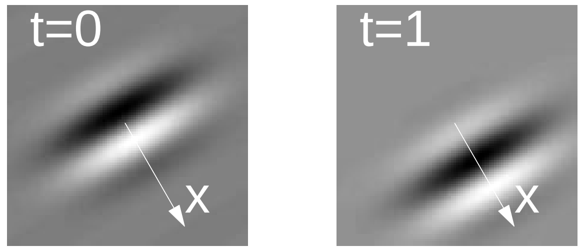
- a flashed bar gives a delayed response




- a moving bar, in one direction, may synchronize responses



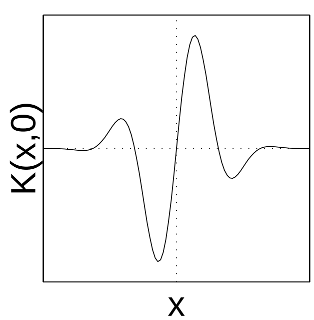
# Separable vs. Inseparable ST RF

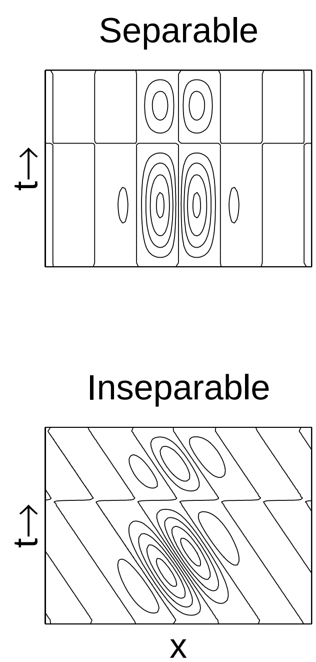



- separable ST RF can be written as

$$
\begin{aligned}
K(x,t) &= (\text{function of space}) \times (\text{function of time}) \\
&= W(x)h(t)
\end{aligned}
$$

- inseparable ST RF cannot be written this way




- only ST inseparable RFs are DS(Reid et al., 1991)

## Response to Sine Gratings (Analysis)

- response of cell to input $I(x,t)$ and ST RF $K(x,t)$:

$$y(t) = \int_{-\infty}^{+\infty} dx' \int_{-\infty}^{t} dt' I(x',t') K(x', t-t')$$

- for a non-DS cell:

$$\max_t y_1^{\text{non-DS}}(t) = \max_t y_2^{\text{non-DS}}(t)$$

- if

$$K(x,t) = W(x)h(t)$$

and

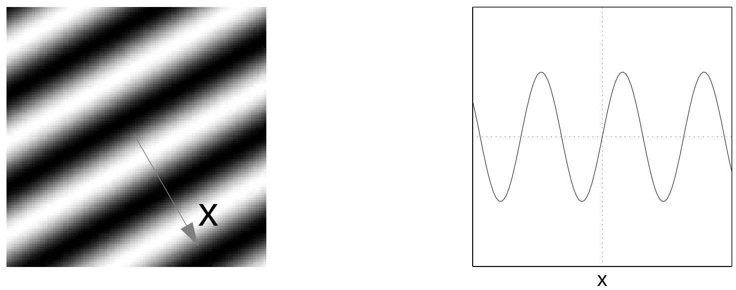
$$\begin{aligned} I_1(x,t) &= \sin(x - vt) \\ I_2(x,t) &= \sin(x + vt) \end{aligned}$$

then, one can show,

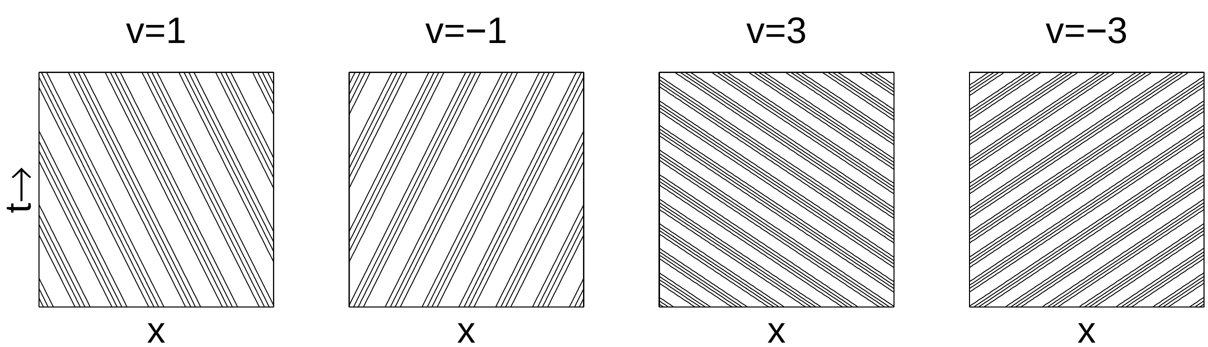
$$\max_t y_1(t) = \max_t y_2(t)$$

# RESPONSE TO SINE GRATINGS (EXAMPLE)

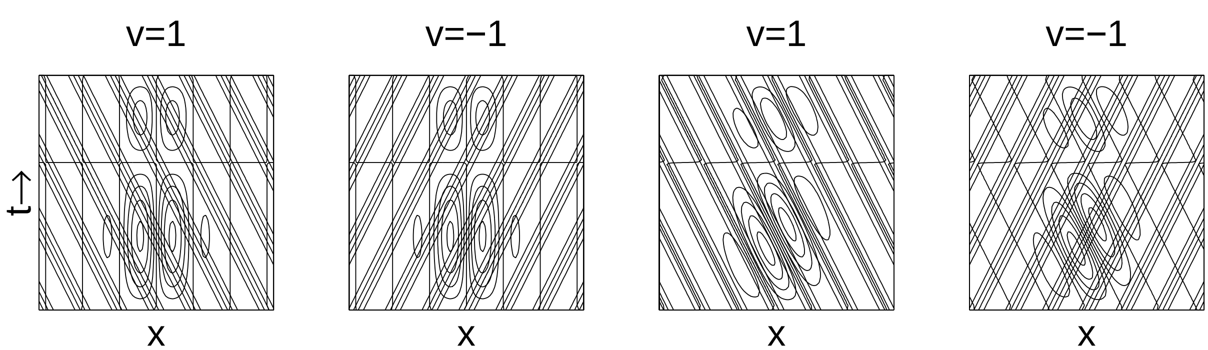
- profile of a sine grating:




- moving sine gratings as (space)-(time) plots:



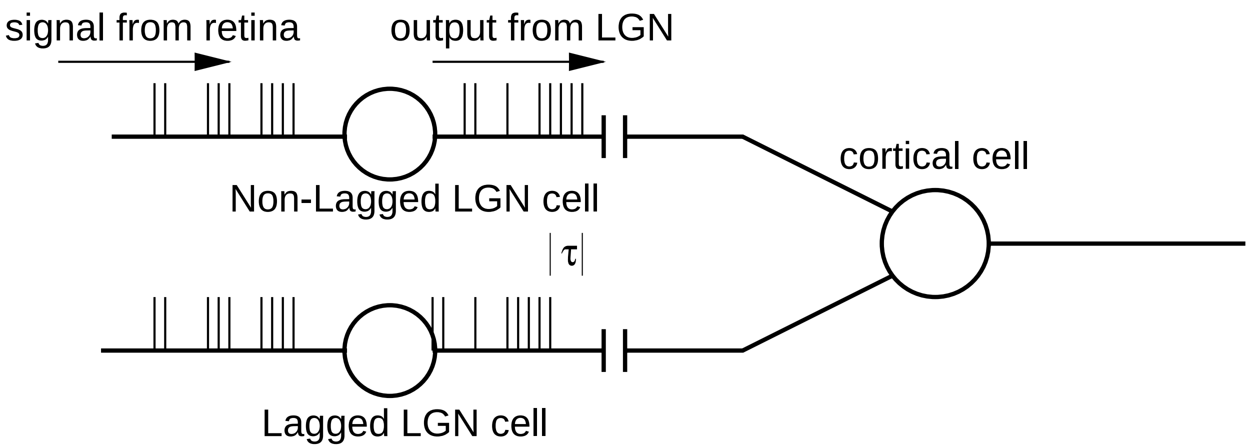

- moving sine gratings overlayed with ST RF:




- only ST inseparable RFs are direction selective

# Model of Direction Selectivity

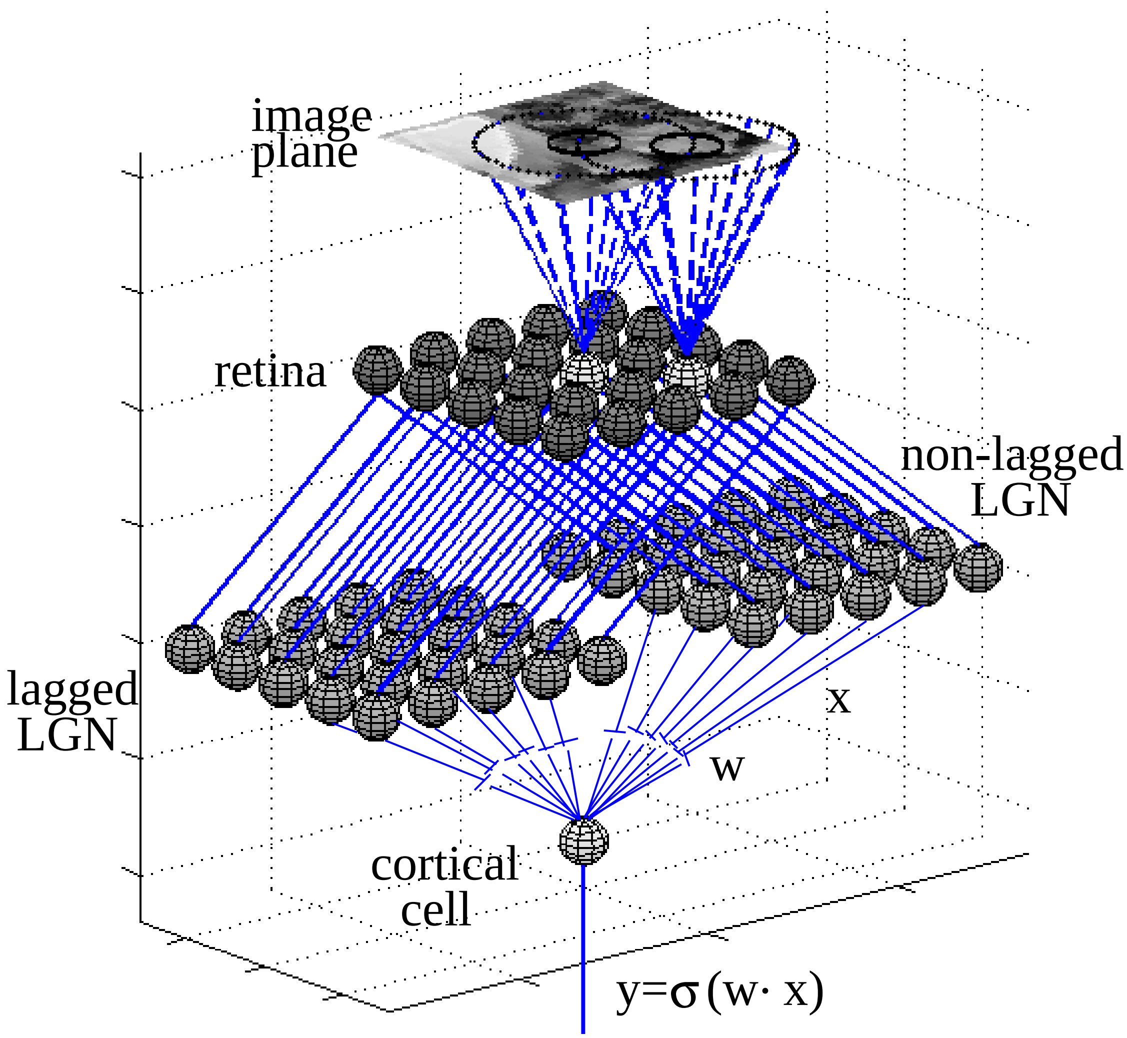
- effects of two types of LGN cells can give rise to DS,(Feidler et al., 1997)
  - lagged
  - non-lagged




- lagged LGN cells have a delayed response

$$\mathbf{x}^{\text{lagged}}(t) = \mathbf{x}^{\text{non-lagged}}(t - \tau)$$

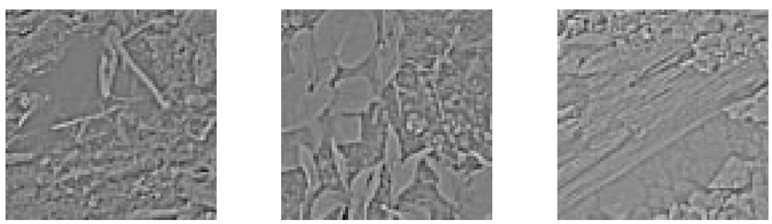
## Model of Direction Selectivity (Architecture)



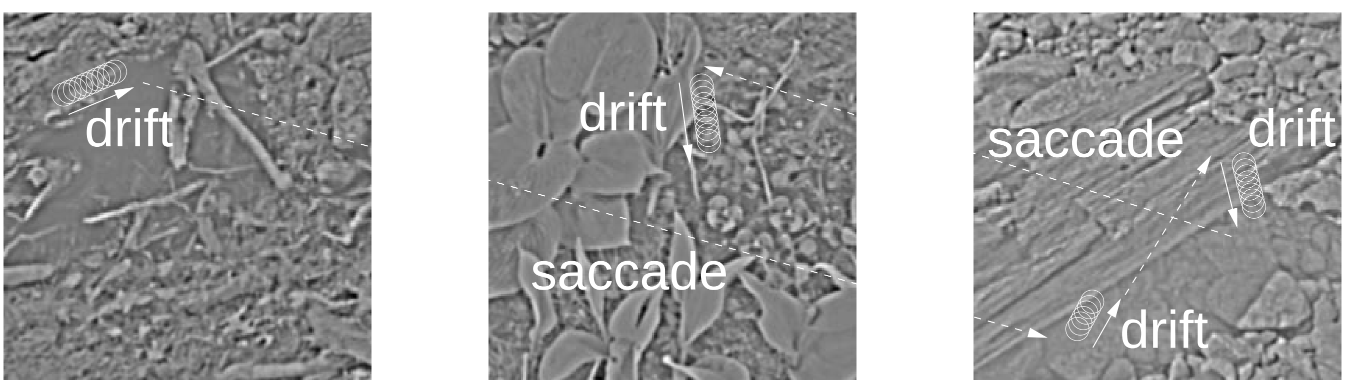
## MODEL OF DIRECTION SELECTIVITY (ENVIRONMENT)

- input patches from natural scenes

- images are processed with a retinal difference of Gaussians (DOG)



- sequence of patches chosen from eye movements
  - drifts
  - saccades



# Model of Direction Selectivity (Learning Rules)

- Quadratic BCM

$$
\begin{aligned}
\frac{d\mathbf{w}}{dt} &= y(y - \Theta_M)\sigma'\mathbf{x} \\
\Theta_M &\equiv E[y^2]
\end{aligned}
$$

- Skewness

$$
\begin{aligned}
\frac{d\mathbf{w}}{dt} &= y(y - \Theta_M)\sigma'\mathbf{x}/\theta_S \\
\Theta_M &\equiv E[y^3]/E[y^2], \theta_S \equiv E^{1.5}[y^2]
\end{aligned}
$$

- Kurtosis

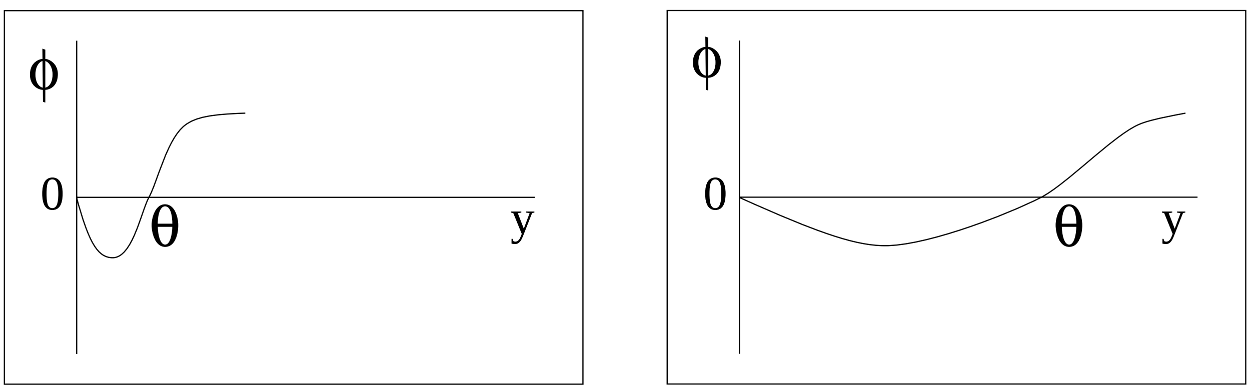
$$
\begin{aligned}
\frac{d\mathbf{w}}{dt} &= y(y^2 - \Theta_M)\sigma'\mathbf{x}/\theta_S \\
\Theta_M &\equiv E[y^4]/E[y^2], \theta_S \equiv E^2[y^2]
\end{aligned}
$$

- PCA

$$
\frac{d\mathbf{w}}{dt} = y(\mathbf{x} - y\mathbf{w})
$$

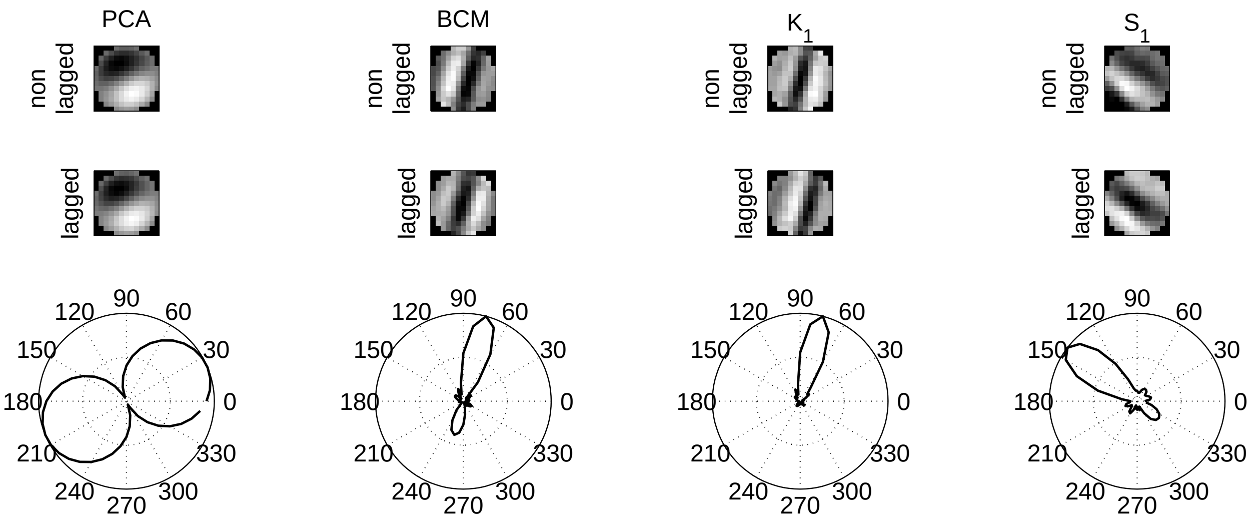
## BCM LEARNING RULES

- negative and positive regions of modification
- threshold which *slides* as a super-linear function of the output



# RECEPTIVE FIELDS AND TUNING CURVES

- example receptive fields, $v = 2$ pixels/iteration



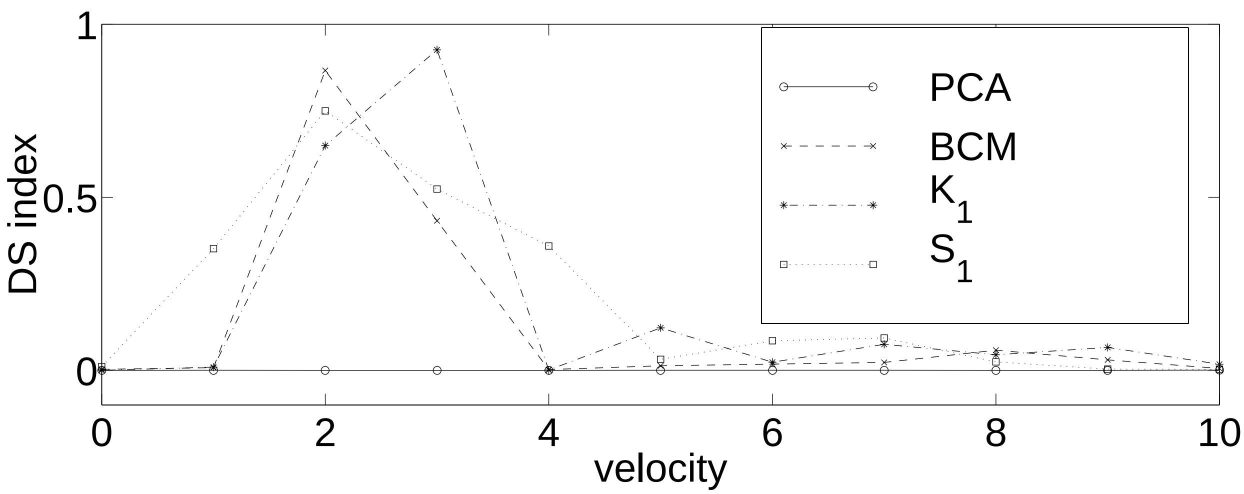

- $K_1$, $S_1$, and BCM neurons developed DS
- PCA neuron did not develop DS

## DRIFT VELOCITY DEPENDENCE

- direction selectivity index

$$\mathrm{DS} \equiv \frac{R_{\text{(preferred)}} - R_{\text{(non preferred)}}}{R_{\text{(preferred)}} + R_{\text{(non preferred)}}}$$

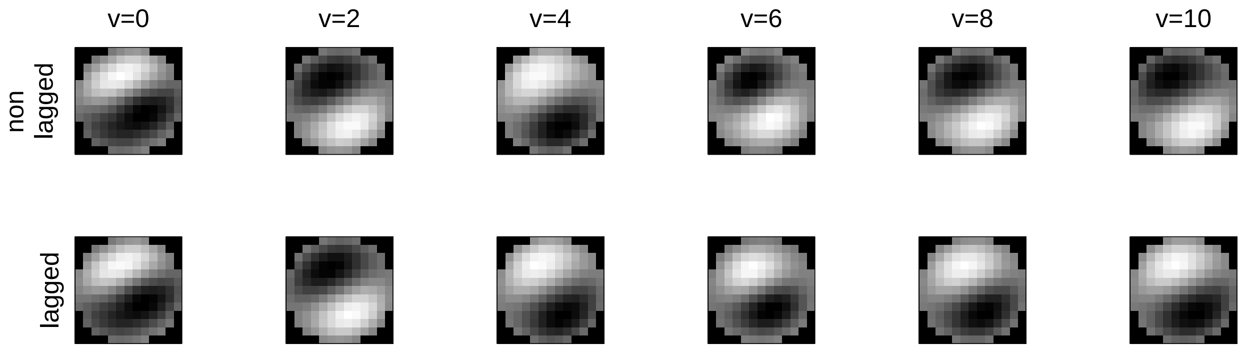
  - $R_{\text{(preferred)}}$ maximum response to an optimal sine grating moving in the preferred direction
  - $R_{\text{(non preferred)}}$ maximum response to the grating moving in the non preferred direction



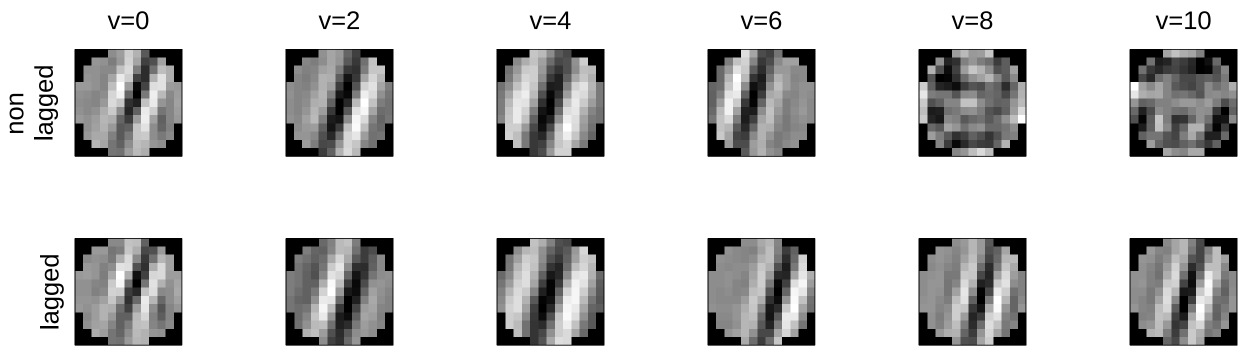

- loss of DS for very high and very low drift velocities

# Receptive Fields and Drift Velocity

- PCA



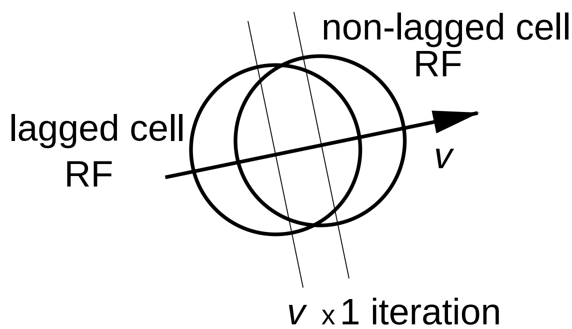

- BCM



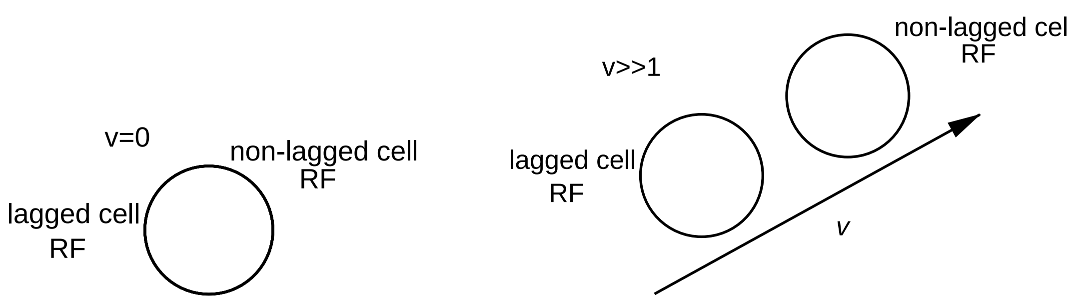

- PCA: RFs always separable
- BCM: $v = 0$, lagged and non-lagged RFs identical
- BCM: $v \gg 1$, one of the lagged or non-lagged RF doesn't develop

# EYE DRIFT AND RF OVERLAP

- drifts with lagged cells $\leftrightarrow$ overlap with two eyes
- during a drift, cell receives input from overlapping RFs

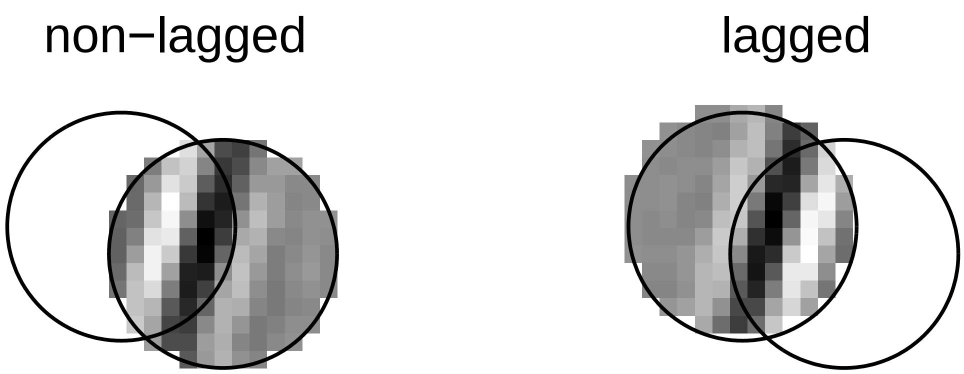



- $v = 0 \Rightarrow$ complete overlap, $v \gg 1 \Rightarrow$ no overlap



## BCM: BINOCULAR OVERLAP AND DS

- (Shouval et al., 1996) on binocular misalignment
  - complete overlap $\Rightarrow$ identical left and right RFs
  - partial overlap $\Rightarrow$ RF forms in overlap area
  - no overlap $\Rightarrow$ only one RF forms (monocular)




- Direction Selectivity and BCM:
  - complete overlap ($v = 0$) $\Rightarrow$ ST separable $\Rightarrow$ no DS
  - partial overlap ($v \neq 0$) $\Rightarrow$ ST inseparable $\Rightarrow$ DS
  - no overlap ($v \gg 1$) $\Rightarrow$ ST separable $\Rightarrow$ no DS

## PCA: Binocular Overlap and DS

– correlation function is symmetric

$$\mathbf{C} = \begin{pmatrix} \mathbf{C}_s(|\mathbf{r}-\mathbf{r}')| & \mathbf{C}_o(|\mathbf{r}-\mathbf{r}'|) \\ \mathbf{C}_o(|\mathbf{r}-\mathbf{r}'|) & \mathbf{C}_s(|\mathbf{r}-\mathbf{r}'|) \end{pmatrix}$$

– left and right eye weights are equal, up to a sign

$$\mathbf{w}(\mathbf{r}) = \begin{pmatrix} \mathbf{w}^{\text{left}}(\mathbf{r}) \\ \pm\mathbf{w}^{\text{left}}(\mathbf{r}) \end{pmatrix}$$

- Direction Selectivity and PCA:
  - correlation function is symmetric $\Rightarrow$ receptive fields are ST separable $\Rightarrow$ no DS
  - (Wimbauer et al., 1997a) and (Wimbauer et al., 1997b) obtain DS using a modified Hebb rule, but...
    - $*$ lagged and non-lagged cells are uncorrelated $\Rightarrow$ loss of orientation selectivity
    - $*$ asymmetric correlation function $\Rightarrow$ motion in environment is biased in particular directions

## CONCLUSIONS FOR DIRECTION SELECTIVITY

- cortical cells receiving input from lagged and non-lagged LGN cells can develop direction selectivity
- DS cannot develop with a simple Hebb rule this way
- BCM, and similar rules, can develop DS
- parallel between eye drift and binocular overlap let's us understand how DS arises