

Formation of Direction Selectivity in Natural Scene Environments

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Abstract

Most simple cells in the cat striate cortex are both orientation and direction selective. In this paper we use single cell learning rules to develop both orientation and direction selectivity in a natural scene environment. We show that a simple PCA rule is inadequate to develop direction selectivity, but that the BCM rule and similar rules can. We compare these models to experiments in motion deprived environments, such as strobe rearing, and show some connections between the development of direction and orientation selectivity.

1 Introduction

Most simple cells in the cat striate cortex are both orientation and direction selective. At the preferred orientation, a cell which is direction selective responds to a drifting grating moving in one direction more strongly than the opposite direction. The ability of the cell to detect the direction of motion depends on the interaction of responses to at least two different points in the visual field at different times. This is to say, that it depends on the *spatiotemporal* receptive field of the cell (Reid et al., 1991).

Spatiotemporal (ST) receptive fields are generally characterized by their degree of separability. A spatiotemporal *separable* receptive field can be expressed as a product of a function which only depends on time and a function which only depends on space. A spatiotemporal *inseparable* receptive field is one that cannot be expressed as such a product.

In order for a cell to be direction selective, it must have a ST inseparable receptive field. This can be seen by a simple example. Consider the spatiotemporal contour plot of a one dimensional ST separable receptive field (Figure 1, left). A temporal cross section made vertically through the contour plot represents the temporal response function to flashed stimulus at a point x . A ST inseparable receptive field would have different response timings at different spatial positions, as in Figure 1, right. A space-time plot of a drifting grating can be superimposed with these contour plots (see Figure 2), from which we can easily see that only a ST inseparable receptive field can be direction selective.

A model of direction selectivity has been proposed (Feidler et al., 1997) which models the effects of two types of LGN cells, called lagged and non-lagged cells, which differ only in their response timing. They conclude that simple Hebbian rules are inadequate to develop direction selectivity, and demonstrate more sophisticated Hebb-type learning rules, such as postsynaptic gating and BCM (Bienenstock et al., 1982), are sufficient to obtain direction selectivity. In this paper we present a model of direction selectivity based on lagged and non-lagged LGN cells, but we use a more realistic input environment than has been previously used. We reproduce the observation that simple Hebb rules are incapable of producing direction selective cells. We also consider several other rules, which have similar form to the BCM rule, and explore how they develop direction selectivity. We then compare these rules to experiments in strobe light environments (Cynander et al., 1973).

2 Methods

We use as the visual environment, 13x13 circular patches from 12 images of natural scenes processed with a retinal DOG filter(Law and Cooper, 1994). The cortical cell receives input from two sets of LGN cells which view the same area of space, but differ only in their timing. The first set has a delayed response to the input (lagged cells) relative to the second set (non-lagged cells). Essentially the cortical cell has a receptive field from two different times of the input at the same spatial location. We will refer to these as the lagged and the non-lagged RFs, because they arise from the lagged LGN and the non-lagged LGN cell inputs, respectively.

The input patches are chosen using a sequence of random *saccades* and *drifts*(Carpenter, 1977). A saccade is a large jump to a random part of an image, and a drift is a continuous motion within an image in a particular direction at a particular velocity. In the model, the drift velocity is kept constant, and the drifts last a random time . In between drifts are saccades to a different image or part of the same image. We observe that the high velocity case in the model is comparable to the strobe light environment, because in both situations the temporal correlations are lost. Thus, results in the high velocity case can be compared to those experiments.

We denote the input vector by \mathbf{d} and the weight vector is \mathbf{m} . Neural activity is given by the rectified product of the inputs and the weights, $c = s(\mathbf{d} \cdot \mathbf{m})$. s' denotes the derivative of the sigmoidal. We consider several synaptic modification rules. The PCA(Oja, 1982) rule is a stabilized Hebb rule, and the other learning rules have the general properties of BCM synaptic modification functions(Bienenstock et al., 1982). BCM synaptic modification functions are characterized by a negative region for small post-synaptic depolarization, a positive region for large post-synaptic depolarization, and a threshold, Θ_M , which moves as a function of the post-synaptic activity and switches between the Hebbian and anti-Hebbian regions.

Quadratic BCM (Intrator and Cooper, 1992)

$$\frac{d\mathbf{m}}{dt} = c(c - \Theta_M)s'\mathbf{d} = c(c - E[c^2])s'\mathbf{d} \quad (2.1)$$

where the average $E[\cdot]$, is calculated using

$$E[c^n(t)] \approx \frac{1}{\tau} \int_{-\infty}^t c^n(t')e^{-(t-t')/\tau} dt'$$

Skewness This rule is based on the statistical measure of skewness.

$$\frac{d\mathbf{m}}{dt} = c(c - E[c^3]/E[c^2])/E^{1.5}[c^2]s'\mathbf{d} \quad (2.2)$$

Kurtosis This rule is based on the statistical measure of kurtosis.

$$\frac{d\mathbf{m}}{dt} = c(c^2 - E[c^4]/E[c^2])/E^2[c^2]s'\mathbf{d} \quad (2.3)$$

PCA

$$\frac{d\mathbf{m}}{dt} = c(\mathbf{d} - c\mathbf{m}) \quad (2.4)$$

3 Results

Example receptive fields and their orientation tuning, for a velocity of 2 pixels per iteration, are shown in Figure 3. The orientation tuning was obtained using drifting oriented sine gratings. It is clear that the PCA rule did not develop direction selectivity whereas the other rules did.

We measure direction selectivity using the DS index, defined as

$$DS \equiv \frac{R_{(\text{preferred})} - R_{(\text{nonpreferred})}}{R_{(\text{preferred})} + R_{(\text{nonpreferred})}} \quad (3.5)$$

where $R_{(\text{preferred})}$ and $R_{(\text{nonpreferred})}$ are the responses to a sine grating, at optimum orientation and spatial frequency, moving in the preferred direction and non preferred direction, respectively. Figure 4 shows the index as a function of eye drift velocity, for a constant LGN lag of 1 iteration. Example receptive fields from the BCM learning rule for each velocity are shown. Other than the PCA rule, all rules show some velocity tuning: they exhibit direction selectivity for some velocities, but all lose it for either velocities which are too high or too low.

4 Summary and Conclusions

We have presented a model for direction selectivity using a realistic input environment, and assuming lagged and non-lagged LGN cell responses. The results confirmed previous work (Feidler et al., 1997). Since the high velocity case in the model is comparable to the strobe light environment, it is consistent with experiment that most rules lose direction selectivity in this case.

There is a curious parallel between these results and the results on binocular cortical misalignment (Shouval et al., 1996). In the misalignment work, it was shown that the BCM rule in a natural scene environment, with varying degrees of binocular overlap, developed either identical receptive fields (for complete overlap), *monocular* receptive fields (for no overlap), or receptive fields formed only in the overlap region (for intermediate overlap). In the current work, if the lag time of the LGN lagged cells is kept constant, then a constant velocity would imply a constant amount of overlap of input patterns during eye drift. Thus, zero velocity would yield identical lagged and the non-lagged RFs, yielding no direction selectivity. Likewise, high velocity would give no overlap of input patterns during eye drift, and would yield either a completely lagged or a completely non-lagged receptive field, and again no direction selectivity.

Though we have focussed on a geniculocortical single-cell model, there is some indication that network effects, especially cortical-cortical interaction, plays a part in the development of direction selectivity. This work can be seen as a first step towards a network model, and as a straightforward way of addressing some of the issues regarding direction selectivity.

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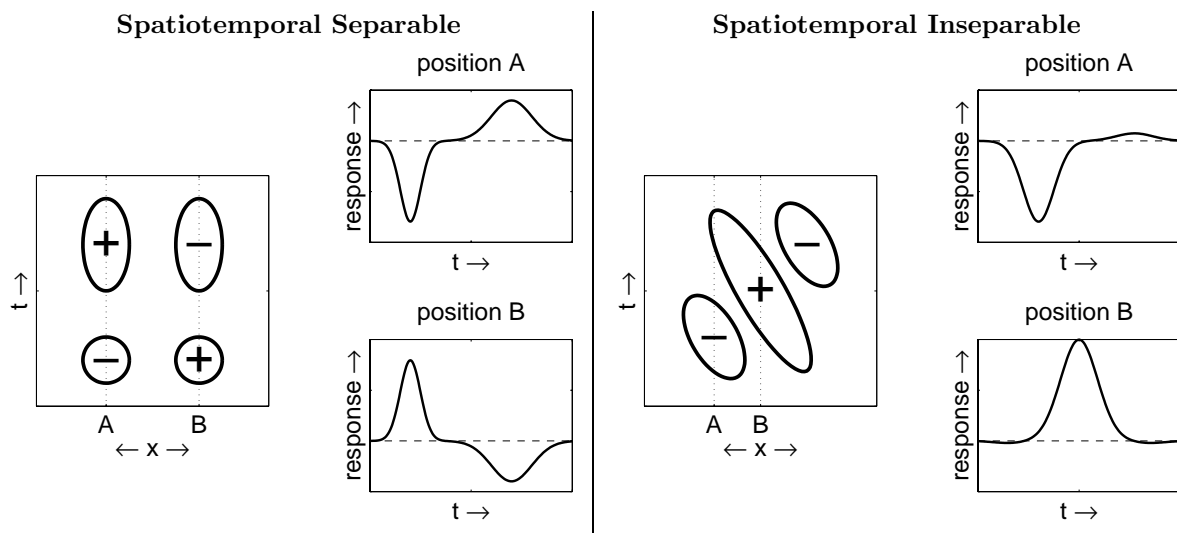


Figure 1: Spatiotemporal contour plots of a one dimensional ST separable receptive field (left) and ST inseparable receptive field (right). A temporal cross section made vertically through the contour plot represents the temporal response function to flashed stimulus at a point x . Example response functions, for points A and B, are shown on the right of each contour plot.

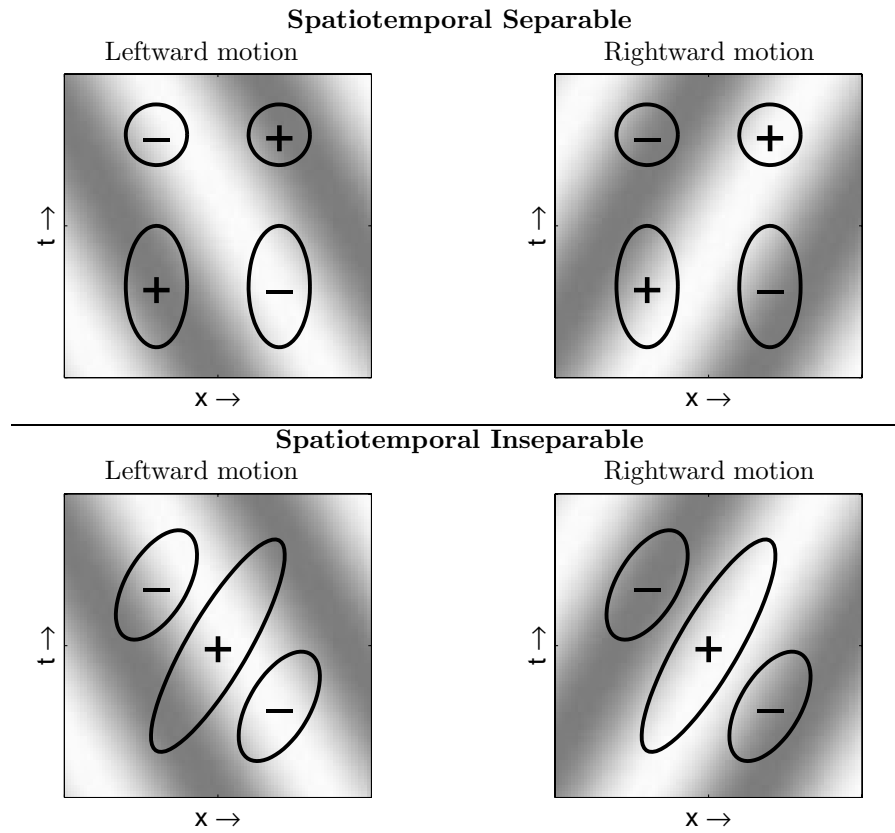


Figure 2: Spatiotemporal receptive field plots of separable (top) and inseparable (bottom) receptive fields, superimposed over spatiotemporal representations of drifting sinusoidal gratings. Gratings appear “oriented” because they shift in a particular spatial direction (x axis) as they move through time (y axis). The response of the cell is the product of the stimulus with the receptive field, summed over both space and time. Thus, for inseparable receptive fields, the stimulus at the preferred space-time “orientation”, i.e. moving the preferred direction of drift, is a more effective stimulus than one moving in the non-preferred direction.

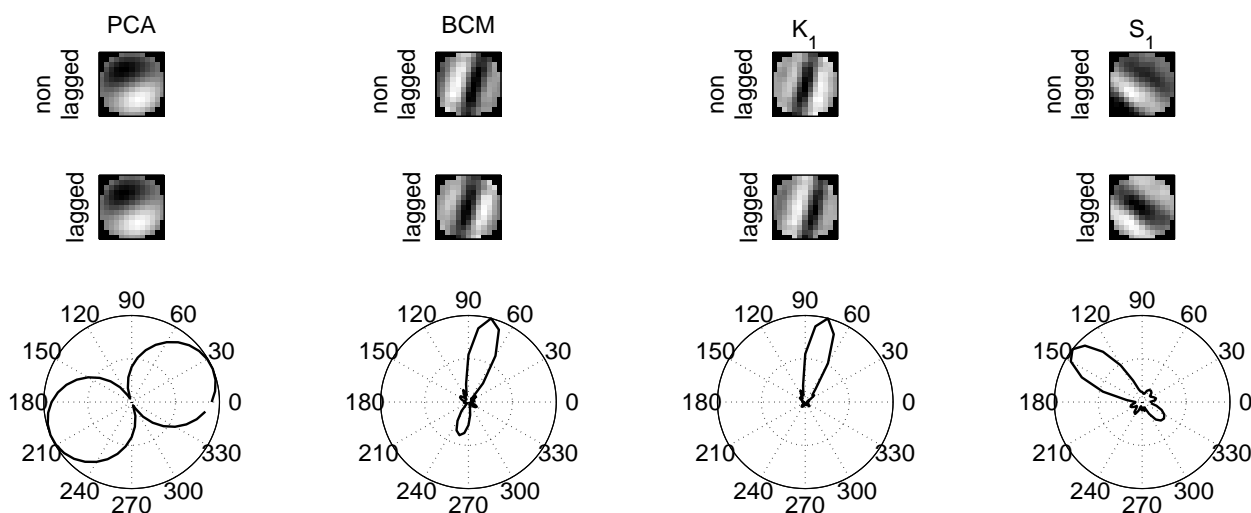


Figure 3: Example receptive fields and their orientation tuning, for a velocity of 2 pixels per iteration. The orientation tuning was obtained using drifting oriented sine gratings. Orientations larger than 180 degrees denotes motion in the opposite direction. Tuning curves which have a larger response for one direction than another are for direction selective cells. The PCA neuron is the only one which did not achieve direction selectivity.

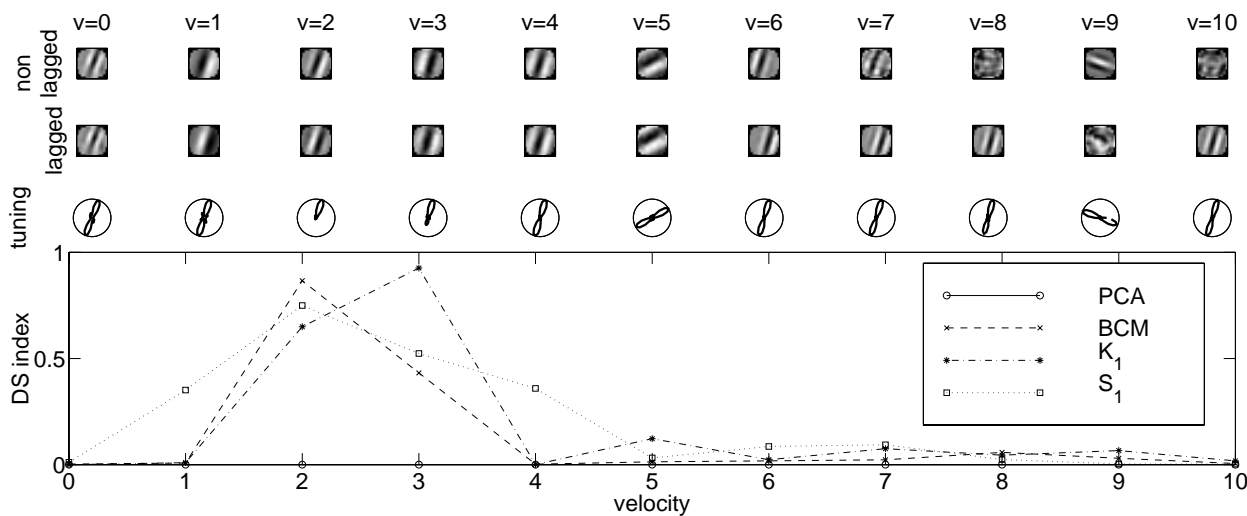


Figure 4: Example receptive fields with polar tuning plots (above) for BCM, for several eye drift velocities. The direction selectivity index as a function of velocity (below) for four different learning rules. The PCA learning rule did not develop direction selectivity. The other rules show some velocity tuning: they all lose direction selectivity for either velocities which are too high or too low. The LGN lagged cells had a constant 1 iteration lag.