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Formation of Direction Selectivity in Natural Scene Environments

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Most simple and complex cells in the cat striate cortex are both orientation and direction selective. In this article we use single-cell learning rules to develop both orientation and direction selectivity in a natural scene environment. We show that a simple principal component analysis rule is inadequate for developing direction selectivity, but that the BCM rule as well as similar higher-order rules can. We also demonstrate that the convergence of lagged and nonlagged cells depends on the velocity of motion in the environment, and that strobe rearing disrupts this convergence, resulting in a loss of direction selectivity.

1 Introduction ---

Most simple and complex cells in the cat striate cortex are both orientation (Hubel & Wiesel, 1959, 1962) and direction selective (Hammond, 1978; Reid, Soodak, & Shapley, 1991; Deangelis, Ohzawa, & Freeman, 1995). At the preferred orientation, a cell that 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).

A cell that is not direction selective (non-DS) has a maximum response to a sine grating moving in one direction equal to its maximum response to a sine grating moving in the opposite direction. In a linear approximation, the response of a cell, $c(t)$, can be written as a convolution between the spatiotemporal input pattern, $I(x, t)$, and a spatiotemporal receptive field kernel, $K(x, t)$, giving

$$c(t) = \int_{-\infty}^{+\infty} dx' \int_{-\infty}^t dt' I(x', t') K(x', t - t'). \quad (1.1)$$

It is easy to show that in this approximation, a DS cell must have a spatiotem-

poral (ST) inseparable receptive field, that is, the kernel cannot be expressed as $K(x, t) = F(t)G(x)$, where $F(t)$ and $G(x)$ are functions that depend on only time and space, respectively.

There are many models of direction selectivity (Barlow & Levick, 1965; Adelson & Bergen, 1985; Watson & Ahumada, 1985; Burr, 1981). In all of the models, the response of the cell is determined by receptive fields that have different temporal response properties at different spatial locations (i.e., spatiotemporal inseparable). This can be realized by the appropriate spatial positioning of the receptive fields and the introduction of temporal shifts. These temporal shifts could possibly arise from delays caused by cortical loops (Suarez, Koch, & Douglas, 1995; Maex & Orban, 1996), phase advances caused by depressing synapses (Chance, Nelson, & Abbott, 1998), or by lagged responses in the lateral geniculate nucleus (LGN; Mastronarde, 1987; Saul & Humphrey, 1990).

In this article we present a feedforward model of the development of direction selectivity, which includes the effects of two types of LGN cells, called lagged and nonlagged cells, that differ only in their response timing. This is similar to a previous model (Feidler, Saul, Murthy, & Humphrey, 1997), differing significantly in the input environment used. The previous model used a neuron with three inputs each with sinusoidally varying activations governed by a single parameter. In our case, we use a natural scene environment (Law & Cooper, 1994), providing a more realistic correspondence with biology and a more direct connection to experiment. We examine two types of visual environments, differing primarily in their temporal properties. In one environment, static natural images are used with a simple model of eye movements to provide motion over the receptive cortical field. In the other, natural image movies are used to provide motion over the receptive field.

Using these more realistic environments, we reproduce the observation of Feidler et al. (1997) that simple Hebb rules are incapable of producing DS cells, and that the BCM rule (Bienenstock, Cooper, & Munro, 1982) is capable of producing DS cells. We also consider several other statistically motivated rules (Blais, Intrator, Shouval, & Cooper, 1998), which have similar form to the BCM rule, and explore how they develop direction selectivity. In addition we provide an insight into the reason that direction selectivity is, or is not, produced by these rules. Finally, we compare these simulations to experiments in strobe light environments (Cynader, Berman, & Hein, 1973; Cynader & Chernenko, 1976; Humphrey & Saul, 1998).

2 Methods

We use as the visual environment 13×13 circular patches from 12 images of natural scenes processed with a retinal difference of gaussian filter (Law & Cooper, 1994). The cortical cell receives input from two sets of lateral geniculate nucleus (LGN) cells that view the same area of space but differ in their timing. The first set has a delayed response to the input (lagged cells)

relative to the second set (nonlagged cells). Essentially the cortical cell has a receptive field that is composed of two different receptive fields that receive input from two different times at the same spatial location. We will refer to these as the lagged and the nonlagged RFs.

Two possible factors contribute to motion in the visual environment: movements of the eyes and head and movements of objects in the world. To model the former, 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. Although this is a simplification of both the temporal properties of lagged and nonlagged cells and of the true input structure available to an animal in a dynamic environment composed of moving objects in addition to eye and head movements, the added complexities make no noticeable difference in the results (see Figure 3). In contrast, the simplification of the environment provides insights that may be obscured in the complexities, and it allows the velocities and delays to be more tightly controlled.

We denote the input vector by \mathbf{d} and the weight vector by \mathbf{m} . Neural activity is given by the rectified product of the inputs and the weights, $c = \sigma(\mathbf{d} \cdot \mathbf{m})$. The derivative of the sigmoidal is given simply by σ' . We consider several synaptic modification rules such as the quadratic form of BCM (Bienenstock et al., 1982; Intrator & Cooper, 1992) as well as other statistically motivated rules that share the basic properties proposed by BCM (Blais et al., 1998). We include, for comparison, a stabilized Hebb rule used for extracting the principal component of the input (PCA) (Oja, 1982). These rules have the form:

Quadratic BCM (Intrator and Cooper, 1992):

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

Skewness [S1]. This rule is based on the statistical measure of skewness:

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

Kurtosis [K1]. This rule is based on the statistical measure of kurtosis:

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

For all of these rules, we replace the spatial average, $E[\cdot]$, by a temporal average of the form

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

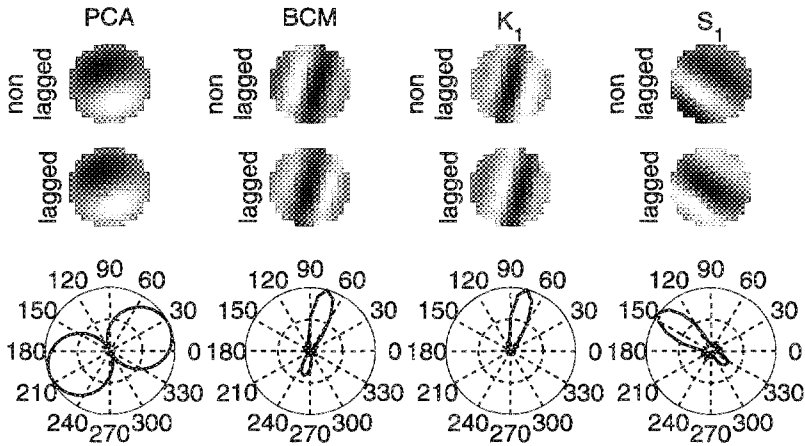


Figure 1: Sample receptive fields and their orientation tuning, for a velocity of two pixels per iteration. The orientation tuning was obtained using drifting oriented sine gratings. Orientations larger than 180 degrees denote motion in the opposite direction. Tuning curves that have a larger response for one direction than another are for direction-selective cells. The PCA neuron is the only one that did not achieve direction selectivity.

PCA

$$\frac{dm}{dt} = c(d - cm). \quad (2.4)$$

We measure direction selectivity using the DS index, defined as

$$DS \equiv \frac{R_{(\text{preferred})} - R_{(\text{nonpreferred})}}{R_{(\text{preferred})} + R_{(\text{nonpreferred})}}, \quad (2.5)$$

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 nonpreferred direction, respectively.

3 Results

Example receptive fields and their orientation tuning, for a drift velocity of 2 pixels per iteration, are shown in Figure 1. 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. A spatiotemporal separable receptive field would be attained if the lagged RF is a simple scalar multiple of the nonlagged RF, such as that observed to occur using the PCA learning rule.

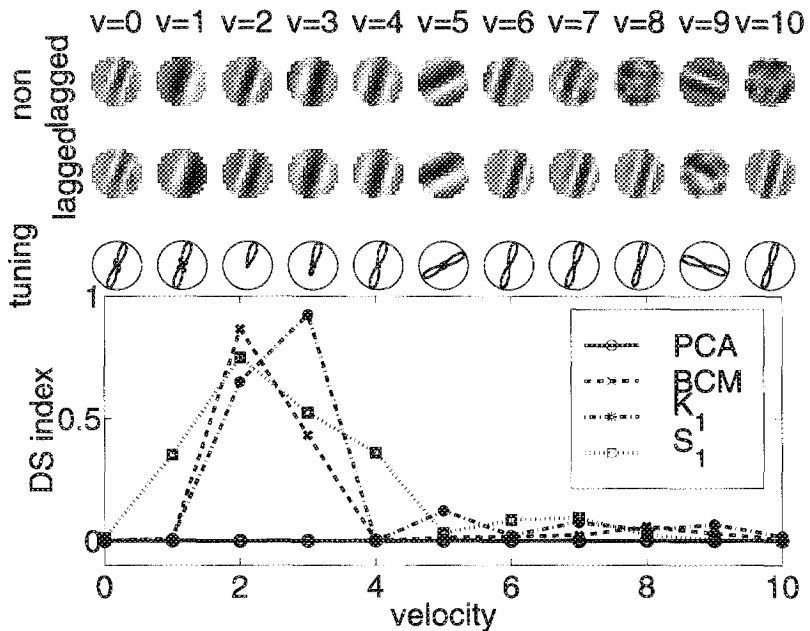


Figure 2: Sample receptive fields with polar tuning plots (above) for BCM, for several eye drift velocities. The direction selectivity index as a function of drift velocity (below) for four different learning rules. The PCA learning rule did not develop direction selectivity. The other rules show some tuning to eye drift velocity; they all lose direction selectivity for velocities that are too high (no overlap) or too low (near complete overlap). The LGN lagged cells had a constant one-iteration lag.

The other learning rules developed different lagged and nonlagged RFs. We observe that the lagged RF is a shifted version of the nonlagged RF, which yields a spatiotemporal inseparable receptive field. Figure 2 shows the direction selectivity index as a function of eye drift velocity, for a constant LGN lag of one iteration. Example receptive fields from the BCM learning rule for each velocity are shown. Other than the PCA rule, all rules show some tuning to eye drift velocity: they develop direction selectivity for some velocities, but all lose it for velocities that are too high or too low. At very low velocities, the lagged and nonlagged RFs are identical (ST separable), and at very high velocities only the lagged or the nonlagged develops while the other RF is small and random (also ST separable).

Using a more dynamic environment (movies from van Hateren & Ruder- man, 1998) and a more realistic temporal filtering (Saul & Humphrey, 1990; Wimbauer, Wenisch, Miller, & von Hemmen, 1997a) does not alter the main

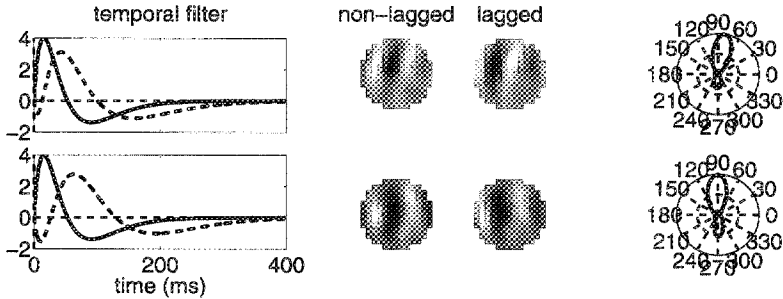


Figure 3: Direction selectivity in a movie environment. Neurons are trained with sequential patches from movies preprocessed with a spatial DOG and temporal filters for lagged and nonlagged cells, as specified in (Wimbauer et. al., 1997a). The BCM rule was used in these examples. Shown are the temporal filters (left), the receptive fields for the lagged and nonlagged channels (middle), and the orientation tuning of the cells (right). The results are comparable to those from the drift-saccade input model.

result (see Figure 3). The neurons develop a spatiotemporal inseparable receptive field and are thus direction selective.

4 Summary and Conclusions

This work extends previous work (Feidler et al., 1997) in which a cell attained direction selectivity in a simplified environment; the authors' conclusion—that a simple Hebb rule is inadequate to develop direction selectivity—is reproduced. Other than the PCA rule, all the rules examined develop direction selectivity for some velocities, but all lose it for velocities that are too high or too low. There is a parallel between these results and the results on binocular cortical misalignment (Shouval, Intrator, Law, & Cooper, 1996), which we explain.

In the misalignment work, it was shown that the BCM rule in a natural scene environment, with varying degrees of binocular overlap, developed 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 nonlagged RFs, yielding no direction selectivity. Similarly, high velocity would give no overlap of input patterns during eye drift and would yield either a completely lagged or a completely nonlagged receptive field, and again no direction selectivity. The high-velocity case is analogous to the strobe light environment (Cy-

nader et al., 1973; Cynader & Chernenko, 1976; Humphrey & Saul, 1998), because in both situations, the temporal correlations are lost. In experiment direction selectivity was lost but orientation selectivity remained, which is reproduced by the simulations for the high-velocity case. In addition, there is evidence (Humphrey, Saul, & Feidler, 1998) that strobe rearing prevents the convergence of the lagged and nonlagged inputs onto the cortical cell—that is, the cortical receptive field is affected by either lagged or nonlagged but not both. This result is reproduced completely in the simulations.

It is straightforward to show that a PCA neuron in a spatially isotropic input environment develops either two identical receptive fields or two receptive fields differing only by a sign.¹ These two cases are, in the context of lagged and nonlagged receptive fields, ST separable and *not* direction selective. A recent model of direction selectivity used a correlation-based learning paradigm, with lagged and nonlagged LGN responses (Wimbauer et al., 1997a; Wimbauer, Wenisch, Miller, & von Hemmen, 1997b). The results were that direction selectivity could not form unless the lagged and nonlagged RFs developed independently (very weak correlations) or if the environment contains anisotropic motion (objects move in some directions more often than others). Despite the added complication of network effects and continuous response properties, these results can be understood from the results presented here using the single-cell PCA neuron. The BCM rule, as well as higher-order rules, as we have seen, require neither of these assumptions to develop direction selectivity.

Recent comparisons between independent component analysis (ICA) or efficient coding of natural image sequences and the ST receptive fields of visual cortical neurons have been performed (van Hateren & Ruderman, 1998; Rao & Ballard, 1997). The assumptions used there were different from the ones used in the current work; however, some of the results are similar. The primary differences are that many more temporal delays are included in the ICA work, and the environment is required to be “whitened.” There are two possible interpretations to that work. One is that there are many different types of LGN neurons, each with a different time lag and each converging through independent synaptic weights on a single cortical cell. This interpretation is similar to our work, differing in our use of only two populations of LGN cells, as indicated experimentally, and in that we have investigated several different learning rules. Another interpretation is that there is one population of LGN cells but that synaptic weights have independent values at different time points. This interpretation is very different from our suggestion and is unlikely biologically.

¹ Simply stated, if the two-channel correlation function is symmetric and has the form $C = \begin{pmatrix} C_1 & C_2 \\ C_2 & C_1 \end{pmatrix}$, then the two channels of the principal components, $\mathbf{v} = \begin{pmatrix} \mathbf{v}_1 \\ \mathbf{v}_2 \end{pmatrix}$, are identical up to a sign, $\mathbf{v}_1 = \pm \mathbf{v}_2$.

In addition, the use of “whitening” can be problematic. Although LGN responses could be approximately decorrelated (Atick & Redlich, 1992; Dan et al., 1996), some of the rules used for ICA are particularly sensitive to small correlations remaining in nearly whitened environments (Blais et al., 1998). Also, for the same interpretations described above, the spatiotemporal whitening performed could be questionable biologically. The learning rules in the current work do not require whitening, nor are they affected adversely by it, and thus they provide a more robust system for achieving direction selectivity. The interpretation of these other works and the comparison to biological quantities are therefore significantly different. The fact that they achieve direction selectivity in the natural scene environment is the same as the current work.

Although we have focused on a geniculocortical single-cell model, there is some indication that network effects, especially cortical-cortical interaction, play a part in direction selectivity (Livingstone, 1998). This work can be seen as a first step toward a network model and as a straightforward way of addressing some of the issues regarding direction selectivity.

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