Re-revised Version (22nd August, 2002) **MS 2543**

An Analysis of Synaptic Normalisation in a General Class of Hebbian Models

Terry Elliott

Department of Electronics and Computer Science,

University of Southampton,

Highfield, Southampton, SO17 1BJ,

United Kingdom.

E-mail: `te@ecs.soton.ac.uk`;

Tel: +44 (0)23 8059 6000;

Fax.: +44 (0)23 8059 3313.

Abbreviated Title: Normalisation in Hebbian Models

Keywords: Synaptic normalisation; Hebbian model; activity-dependent competition; neuronal development; mathematical models.

Abstract

In standard Hebb models of developmental synaptic plasticity, synaptic normalisation must be introduced in order to constrain synaptic growth and ensure the presence of activity-dependent, competitive dynamics. In such models, multiplicative normalisation cannot segregate afferents whose patterns of electrical activity are positively correlated, while subtractive normalisation can. It is now widely believed that multiplicative normalisation cannot segregate positively correlated afferents in any Hebb model. However, we recently provided a counter-example to this belief by demonstrating that our own neurotrophic model of synaptic plasticity, which can segregate positively correlated afferents, can be reformulated as a non-linear Hebb model with competition implemented through multiplicative normalisation. We now perform an analysis of a general class of Hebb models under general forms of synaptic normalisation. In particular, we extract conditions on the forms of these rules that guarantee that such models possess a fixed point structure permitting the segregation of all but perfectly correlated afferents. We find that the failure of multiplicative normalisation to segregate positively correlated afferents in a standard Hebb model is quite atypical.

1 Introduction

Activity-dependent competition between afferent cells, leading to the segregation of afferents' arbors on their target structures, is a ubiquitous feature of the developing vertebrate nervous system (Purves & Lichtman, 1985). In order to construct a mathematical model of neuronal development that includes such competitive dynamics, it is well known that a standard Hebb growth rule by itself is insufficient. This is because such a rule typically leads to the unconstrained growth of all afferents on all of their target cells. In order to implement competition, developmental models frequently employ post-synaptic normalisation, a procedure by which it is assumed that post-synaptic or target cells constrain their total afferent input to remain at or below some limit. Thus, one afferent's gain is at the other afferents' loss and competition is achieved at the same time as constraining growth.

The classic form of synaptic normalisation is multiplicative normalisation (von der Malsburg, 1973). Under multiplicative normalisation, a standard Hebb growth rule is modified to include a decay term proportional to the strength (or efficacy or weight) of the afferent input, the constant of proportionality being chosen so that there is no overall synaptic growth at each target cell. However, it is well known that while multiplicative normalisation in a standard Hebb model does segregate afferents whose patterns of electrical activity are anti-correlated, it does not segregate positively correlated afferents (but see von der Malsburg & Willshaw, 1981). It is likely, however, that a model of neuronal development should be able to segregate positively correlated afferents. For example, the development of ocular dominance columns (Hubel & Wiesel, 1962) in kittens occurs in the presence of correlated vision in both eyes. More generally, from a theoretical viewpoint, it is desirable that self-organising topographic feature maps (Kohonen, 1995) should be able to develop appropriate structures even when the input patterns are positively correlated.

This deficiency of multiplicative normalisation led to the introduction of subtractive normalisation (Goodhill & Barrow, 1994; Miller & MacKay, 1994). Under subtractive normalisation, the standard Hebb growth rule is instead modified so that a decay term independent of the particular afferent input is introduced, the decay term again being chosen so that the total synaptic input to a target cell remains fixed. Unlike multiplicative normalisation, subtractive normalisation does segregate positively correlated afferents. From a biological perspective, however, subtractive normalisation is difficult to motivate, because if synaptic decay processes underlie normalisation, then it is rather improbable that these processes should be independent of the local concentrations of any of the substances that together contribute to synaptic strength. In contrast, while multiplicative normalisation may have its own problems, at least the decay processes are concentration-dependent. Thus, we are impaled on the horns of a dilemma, one horn corresponding to a normalisation rule that does segregate positively correlated afferents but that is biologically implausible, the other horn corresponding to a normalisation rule that does not segregate positively correlated afferents but that is not biologically implausible. Some models that can segregate positively correlated afferents resolve this dilemma by employing significant modifications of the standard Hebb rule (Bienenstock *et al.*, 1982; Harris *et al.*, 1997).

In our own attempt to overcome these problems, we developed an alternative developmental model inspired by biological data implicating a class of molecular factors, the neurotrophic factors, in activity-dependent synaptic competition (for review, see McAllister *et al.*, 1999). This model does segregate positively correlated afferents (Elliott & Shadbolt, 1998). Recently, we have shown that the model can be reformulated as a non-linear Hebb growth rule with competition implemented through multiplicative synaptic normalisation (Elliott & Shadbolt, 2002). This result explicitly contradicts the now wide-spread belief that multiplicative normalisation cannot segregate positively correlated afferents in any Hebb model. Synaptic normalisation was not imposed in our original model (Elliott & Shadbolt, 1998), but rather emerges dynamically (Elliott & Shadbolt, 2002). This emergence hinges on the fact that the model's dynamics decouple into two subspaces, with the competitive dynamics residing in a subspace in which the total synaptic input to target cells (a synaptic scale parameter) plays no role. We argued, moreover, that any model whose competitive dynamics exhibit such scale independence can be recast as a general Hebb growth rule coupled with some form of synaptic normalisation, and that, therefore, synaptic normalisation appears to be an acceptable, abstract mechanism for implementing competitive dynamics in a Hebb model.

We presented our results as an existence proof of a model utilising multiplicative normalisation that can segregate all but perfectly correlated afferents (Elliott & Shadbolt, 2002). We did not perform a more general analysis, seeking to explicate the reasons for our model's capacity to segregate positively correlated afferents under multiplicative normalisation. To this end, we now perform an analysis of a general class of Hebb growth rules coupled with general forms of synaptic normalisation. In particular, we derive a set of conditions on the forms of these rules that guarantee that these models possess a fixed point structure permitting the segregation of all but perfectly correlated afferents. Surprisingly, we find that these conditions are rather easily satisfied. Indeed, the conditions are so easily satisfied that the failure of multiplicative normalisation to segregate positively correlated afferents under a standard Hebb rule is seen to be quite unusual and atypical.

2 Analysis of Models

We consider the dynamics of synaptic competition on a pointwise basis, at single target cells with no coupling between target cells. We may therefore restrict to a consideration of just one target cell. We consider n afferent cells innervating this target cell. Let letters such as i and j label afferent cells, so that, for example, $i = 1, \ldots, n$. Let the number of synapses (or synaptic efficacy or synaptic weight) between afferent cell i and the target cell be denoted by v_i, and let the electrical activity of this afferent cell be denoted by a_i; we take $a_i \geq 0 \; \forall i$. Let the vectors $\mathbf{v}$ and $\mathbf{a}$ be given by $\mathbf{v} = (v_1, \ldots, v_n)^{\mathrm{T}}$ and $\mathbf{a} = (a_1, \ldots, a_n)^{\mathrm{T}}$, where T denotes the transpose. Let the variable t denote time, and let a dot over a variable denote differentiation with respect to time, so that, for example, $\dot{v}_i = dv_i/dt$.

We consider a general class of synaptic growth rules of the form

$$\dot{v}_i = \pi(v_i, a_i) \, \Pi(\mathbf{a} \cdot \mathbf{v}), \tag{1}$$

where $\mathbf{a} \cdot \mathbf{v}$ denotes the dot product between $\mathbf{a}$ and $\mathbf{v}$, $\mathbf{a} \cdot \mathbf{v} = \sum_i a_i \, v_i$. We assume that the functions π and Π are both non-negative, i.e., $\pi(x, y) \geq 0 \; \forall x, y$ and $\Pi(x) \geq 0 \; \forall x$. The term $\pi(v_i, a_i)$ represents a function of a purely pre-synaptic element, while the term $\Pi(\mathbf{a} \cdot \mathbf{v})$ represents a function of a purely post-synaptic element. We have made the simplifying but standard assumption that the post-synaptic response of the target cell is some function of $\mathbf{a} \cdot \mathbf{v}$, the afferent input weighted by the number of synapses (or synaptic efficacy). The form of the synaptic growth rule in Eq. (1) is just that of a product between a pre-synaptic term and a post-synaptic term, and thus is Hebbian in character.

It is well known that such synaptic growth rules typically result in unconstrained synaptic growth, with each v_i growing unboundedly, and that synaptic normalisation must be introduced to constrain the growth and to ensure the presence of competitive dynamics in the models. We consider a general implementation of synaptic normalisation. In particular, we require that

$$\sum_i f(v_i) = 1, \tag{2}$$

where f is some invertible function. Typically, modellers take $f(x) = x$ or $f(x) = x^2$, but we shall consider more general cases. The growth rule in Eq. (1) is then modified so as to ensure that the dynamics respect Eq. (2). We achieve this by replacing Eq. (1) by

$$\dot{v}_i = \pi(v_i, a_i)\, \Pi(\mathbf{a} \cdot \mathbf{v}) - g(v_i)A, \tag{3}$$

where g is some function and the time-dependent quantity A is selected so that

$$\frac{d}{dt} \sum_i f(v_i) = \sum_i f'(v_i)\, \dot{v}_i = 0, \tag{4}$$

where a prime always denotes differentiation with respect to the argument of the associated function. Thus,

$$A = \Pi(\mathbf{a} \cdot \mathbf{v}) \frac{\sum_j f'(v_j)\pi(v_j, a_j)}{\sum_j f'(v_j)g(v_j)}, \tag{5}$$

and our final equation for the evolution of the v_i is given by

$$\dot{v}_i = \Pi(\mathbf{a} \cdot \mathbf{v}) \left[\pi(v_i, a_i) - g(v_i) \frac{\sum_j f'(v_j)\pi(v_j, a_j)}{\sum_j f'(v_j)g(v_j)} \right]. \tag{6}$$

We assume that the functions f and g are both non-negative, i.e., $f(x) \geq 0$, $g(x) \geq 0 \ \forall x$. Because f is invertible, f' is of constant sign, so the denominator in Eq. (6) cannot vanish.

Finally, we make the assumption that the pre-synaptic function $\pi(v_i, a_i)$ is separable as a function of its two arguments. In particular, we assume that

$$\pi(v_i, a_i) = \rho(a_i)\sigma(v_i). \tag{7}$$

Such an assumption simplifies our analysis and guarantees that $\pi(0, a_i) = 0$ provided that $\sigma(0) = 0$, as will later be seen to be required. As we assume that the function π is non-negative, we assume that this is achieved by both ρ and σ being non-negative, i.e., $\rho(x) \geq 0$, $\sigma(x) \geq 0 \; \forall x$.

We analyse Eq. (6) in order to find conditions on the functions Π, ρ, σ, f and g such that solutions exist in which all but one of the v_i are zero. Such solutions correspond to final, segregated states in which all other afferent input has been competitively eliminated in an activity-dependent manner. We insist that these solutions correspond to strictly stable fixed points of Eq. (6) for all but perfectly correlated afferent activity patterns. We also examine the possible existence of unsegregated final states in which two or more afferents innervate the target cell equally. When such states are fixed points of the dynamics, we find that the strict stability of the segregated states forces all such unsegregated fixed points to be unstable. Our analysis thus consists in a fixed point analysis around these segregated and unsegregated states, determining conditions on the functions Π, ρ, σ, f and g such that these states embody the required, activity-dependent, competitive dynamics. We address the question of the possible existence of oscillatory solutions in Section 3.

We proceed, for concreteness, in steps of increasing generality. First we consider the minimal multiplicative model in which all five functions Π, ρ, σ, f and g are the identity function, i.e., $\Pi(x) = x$, etc. We then consider the more general multiplicative model in which f and g are the identity function but Π, ρ and σ are unknown. Finally we consider the fully general model is which all five functions are unknown.

2.1 Minimal Multiplicative Model

For the minimal model, we take Π, ρ, σ, f and g all to be the identity function, i.e., they leave their arguments unchanged. Eq. (6) then becomes

$$\dot{v}_i = v_i \left(\mathbf{a} \cdot \mathbf{v}\right) \left[a_i - \left(\mathbf{a} \cdot \mathbf{v}\right)\right] \tag{8}$$

with $\sum_i v_i = 1$. We average this equation over the ensemble of afferent activity patterns. Defining the symmetric matrix $\mathbf{C}$ with components

$$C_{ij} = \langle a_i a_j \rangle \tag{9}$$

where the angle brackets $\langle\rangle$ denote ensemble averaging, and dropping, for notational convenience, these brackets around the v_i, we then have

$$\dot{v}_i = v_i \left[(\mathbf{C}\mathbf{v})_i - \mathbf{v} \cdot \mathbf{C}\mathbf{v}\right]. \tag{10}$$

Consider the point $\mathbf{u} = (0, \ldots, 0, 1, 0, \ldots, 0)^{\mathrm{T}}$, where only the i^{th} element of $\mathbf{u}$, u_i, is unity, i.e., $u_j = \delta_{ij}$, the Kronecker delta. Expand about this segregated point by writing $\mathbf{v} = \mathbf{u} + \delta\mathbf{v}$, where $\mathbf{n} \cdot \delta\mathbf{v} = 0$, with $\mathbf{n} = (1, \ldots, 1)^{\mathrm{T}}$. For $j \neq i$, after linearising, we obtain

$$\delta\dot{v}_j = \delta v_j (C_{ji} - C_{ii}), \tag{11}$$

with the equation for $\delta\dot{v}_i$ following from $\delta\dot{v}_i = -\sum_{j \neq i} \delta\dot{v}_j$. The points $\mathbf{u}$, $i = 1, \ldots, n$, are therefore all fixed points, and are stable provided that $C_{ii} \geq C_{ji}$ $\forall i, j \neq i$. These points are strictly stable if $C_{ii} > C_{ji}$ $\forall i, j \neq i$, and for our results to be applicable to the full, non-linear case, we require that the strict inequality holds. This condition is simply the statement that each entry on the diagonal of $\mathbf{C}$ is the largest in the corresponding column (and also row, since $\mathbf{C}$ is symmetric).

If the condition $C_{ii} > C_{ji}\ \forall i, j \neq i$ cannot be met for reasonable and natural patterns of afferent activity, then the minimal multiplicative model is incapable of exhibiting the required competitive dynamics, because it would lack the required fixed point structure. What are the characteristic features of those ensembles that do satisfy this condition? Let letters such as α and β label members of the ensemble, so that, for example, $\mathbf{a}^\alpha$ is the α^{th} activity pattern in an ensemble of m patterns. The correlation matrix $\mathbf{C}$ is then given by

$$\mathbf{C} = \frac{1}{m} \sum_{\alpha=1}^{m} \mathbf{a}^\alpha \mathbf{a}^{\alpha\,\mathrm{T}}, \tag{12}$$

and the condition $C_{ii} > C_{ji}\ \forall i, j \neq i$ becomes

$$\sum_{\alpha=1}^{m} (a_i^\alpha)^2 > \sum_{\alpha=1}^{m} a_i^\alpha a_j^\alpha \quad \forall i, j \neq i. \tag{13}$$

Let the vector $\mathbf{A}_i = (a_i^1, \ldots, a_i^m)^{\mathrm{T}}$ be the vector formed from all the values of afferent i's activity over the whole ensemble. We then require that

$$\mathbf{A}_i \cdot \mathbf{A}_i > \mathbf{A}_i \cdot \mathbf{A}_j \quad \forall i, j \neq i. \tag{14}$$

What is the form of the set of vectors $\mathbf{A}_i$, $i = 1, \ldots, n$, that guarantees that this condition is satisfied? If $|\mathbf{A}_i| = |\mathbf{A}_j|$ and $\mathbf{A}_i \neq \mathbf{A}_j\ \forall i, i \neq j$, then this condition is always satisfied. In particular, if all afferents are treated in an unbiased manner, so that the ensemble of activity patterns that they experience is invariant under a uniform translation in the space of afferents, then the various vectors $\mathbf{A}_i$ will all be related through simple permutations of their components, so that, for $i \neq j$, $\mathbf{A}_i = \mathbf{R}_{ij} \mathbf{A}_j$ for some permutation matrix $\mathbf{R}_{ij}$. Translation invariance of the ensemble of afferent activity patterns is an assumption widely made in the modelling literature, and is therefore a reasonable one. Such ensembles are generated, for example, by constructing a basic pattern of activity and applying it by centering it on each afferent in turn. For simplicity, in what follows we shall assume that an ensemble of afferent activity patterns is generated from only one such basic pattern, although because ensemble averaging is a linear function over the ensemble, any results that apply to one such basic pattern will also apply to any number of basic patterns.

We now consider the possible existence of an unsegregated state in which $l > 1$ afferents innervate the target cell equally in the final state. For unbiased activity patterns, unsegregated but unbalanced final states of innervation cannot exist and are therefore not considered. Without loss of generality, we may consider the state

$$\mathbf{u} = \frac{1}{l}(\underbrace{1, \ldots, 1}_{l}, \underbrace{0, \ldots, 0}_{n-l})^{\mathrm{T}} \tag{15}$$

i.e., $u_i = \frac{1}{l}$, $i \leq l$ and $u_i = 0$, $i > l$. Expand about this state as usual, writing $\mathbf{v} = \mathbf{u} + \delta\mathbf{v}$ with $\mathbf{n} \cdot \delta\mathbf{v} = 0$. For this state to be a fixed point, $\mathbf{C}$ must satisfy

$$(\mathbf{Cu})_i = \mathbf{u} \cdot \mathbf{Cu} \quad i \leq l. \tag{16}$$

Defining $\tilde{\mathbf{C}}$ to be the upper $l \times l$ submatrix of $\mathbf{C}$, and $\mathbf{n}_l$ to be the l-dimensional vector with all components unity, this equation simply states that if $\mathbf{u}$ is a fixed point of the dynamics, then $\mathbf{n}_l$ must be an eigenvector of $\tilde{\mathbf{C}}$ with eigenvalue $\frac{1}{l}\mathbf{n}_l \cdot \tilde{\mathbf{C}}\mathbf{n}_l$. Because $\tilde{C}_{ij} \geq 0 \; \forall i, j$, this eigenvalue is positive and is, in fact, the largest eigenvalue of the matrix $\tilde{\mathbf{C}}$. Provided that Eq. (16) is satisfied, we then obtain for $l < n$

$$\delta\dot{v}_i = \begin{cases} \frac{1}{l}\left[(\mathbf{C}\delta\mathbf{v})_i - 2\,\delta\mathbf{v} \cdot \mathbf{Cu}\right] & i \leq l \\ \delta v_i \left[(\mathbf{Cu})_i - \mathbf{u} \cdot \mathbf{Cu}\right] & i > l \end{cases} \tag{17}$$

and for $l = n$

$$\delta\dot{\mathbf{v}} = \frac{1}{n}\mathbf{C}\,\delta\mathbf{v} \tag{18}$$

as the linearised equations for the evolution of $\delta\mathbf{v}$ about $\mathbf{u}$.

Consider first the case $l < n$. For $i > l$, the matrix determining the linear evolution is diagonal with no coupling in the lower left $(n-l) \times l$ block of the matrix to the other v_i's, $i \leq l$, so $n - l$ eigenvalues can be read off immediately. The remaining l eigenvalues are just the eigenvalues of the upper $l \times l$ submatrix of the full matrix, which we denote by $\hat{\mathbf{C}}$. Using Eq. (16) to simplify the terms in δv_i, $i \leq l$, in the expression $\delta\mathbf{v} \cdot \mathbf{Cu}$, we have that

$$\hat{C}_{ij} = \frac{1}{l}\left[\tilde{C}_{ij} - 2\,\mathbf{u} \cdot \mathbf{Cu}\right]. \tag{19}$$

Thus, $\mathbf{n}_l$ is an eigenvector of $\hat{\mathbf{C}}$ with negative eigenvalue $-(\frac{1}{l})^2 \mathbf{n}_l \cdot \tilde{\mathbf{C}}\mathbf{n}_l$ if it is an eigenvector of $\tilde{\mathbf{C}}$. Moreover, if $C_{ii} > C_{ji}\ \forall i, j \neq i$, as required by the strict stability of segregated fixed points, then we also have $\hat{C}_{ii} > \hat{C}_{ji}\ \forall i, j \neq i$. Given these conditions, it is easy to prove that $\hat{\mathbf{C}}$ has a positive eigenvalue. As $\hat{\mathbf{C}}$ is symmetric, its eigenvalues can be characterised variationally, and, in particular, the largest eigenvalue not associated with the eigenvector $\mathbf{n}_l$ is the maximum of $\mathbf{w}\cdot\hat{\mathbf{C}}\mathbf{w}/\mathbf{w}\cdot\mathbf{w}$ over the set of non-zero vectors $\mathbf{w}$ orthogonal to $\mathbf{n}_l$. Consider a vector $\mathbf{w}$ with i^{th} component $+1$ and j^{th} component -1, with all other components zero. Clearly $\mathbf{n}_l \cdot \mathbf{w} = 0$ and we have that $\mathbf{w} \cdot \hat{\mathbf{C}}\mathbf{w}/\mathbf{w} \cdot \mathbf{w} = \frac{1}{2}(\hat{C}_{ii} + \hat{C}_{jj} - 2\hat{C}_{ij})$. Provided that $\hat{C}_{ii} > \hat{C}_{ji}\ \forall i, j \neq i$, as required by the strict stability of the segregated fixed points, then $\mathbf{w} \cdot \hat{\mathbf{C}}\mathbf{w}/\mathbf{w} \cdot \mathbf{w} > 0$, and so $\hat{\mathbf{C}}$ has a positive eigenvalue. Thus, if the point $\mathbf{u}$ is a fixed point, then it is an unstable fixed point provided that the segregated fixed points are strictly stable. These arguments are clearly valid for any submatrix $\tilde{\mathbf{C}}$, not just the upper submatrices.

For the $l = n$ case, $\mathbf{C}$ has a positive eigenvalue associated with the eigenvector $\mathbf{n}$. However, $\mathbf{n} \cdot \delta\mathbf{v} \equiv 0$, so the sign of this eigenvalue is irrelevant to the stability analysis. The matrix $\mathbf{C}$ is, in fact, positive semi-definite, for if $\mathbf{e}$ is an eigenvector with eigenvalue λ, then

$$\lambda|\mathbf{e}|^2 = \mathbf{e}^{\mathrm{T}}\mathbf{C}\mathbf{e} = \frac{1}{m}\sum_{\alpha=1}^{m} |\mathbf{e}\cdot\mathbf{a}^{\alpha}|^2 \geq 0,$$

so all eigenvalues are non-negative.[1] To establish the existence of at least one further, strictly positive eigenvalue, the same variational argument as above shows that $\mathbf{C}$ has a positive eigenvalue associated with an eigenvector orthogonal to $\mathbf{n}$. Indeed, if $n-1$ eigenvalues of $\mathbf{C}$ were identically zero, then $\mathbf{C}$ would be a rank 1 matrix with $\mathbf{C} \propto \mathbf{n}\mathbf{n}^{\mathrm{T}}$, and such a matrix can only be formed by taking $\mathbf{a}^{\alpha} \propto \mathbf{n}$, $\forall\alpha$, i.e., all afferents' activities are perfectly correlated. Thus, if the unsegregated state with $l = n$ is a fixed point, then it is an unstable fixed point.

For which values of l are the states defined by Eq. (15) guaranteed to be fixed points? Provided that afferents are treated in an unbiased manner, so that $C_{ii} = C_{jj}$ $\forall i \neq j$, i.e., $|\mathbf{A}_i| = |\mathbf{A}_j|$ $\forall i \neq j$, then the $l = 2$ and the $l = n$ states are guaranteed to be fixed points. For $l = 2$, this is because any submatrix $\tilde{\mathbf{C}}$ will always be of the form

$$\begin{pmatrix} A & B \\ B & A \end{pmatrix} \tag{20}$$

and thus $(1,1)^{\mathrm{T}}$ is always an eigenvector, satisfying the condition for the $l = 2$ state to be a fixed point. For $l = n$, $\mathbf{n}$ is always an eigenvector of $\mathbf{C}$ if

$$\frac{1}{m}\sum_{\beta=1}^{m} a_i^{\beta} = \frac{1}{n}\sum_{j=1}^{n} a_j^{\alpha} \quad \forall i, \alpha, \tag{21}$$

i.e., if the mean of any pattern's activity over all afferents equals the mean of any afferent's activity over all patterns. Such a condition is always satisfied for the unbiased patterns discussed above, so the $l = n$ state is always a fixed point.

---

[1] An identical argument shows that $\tilde{\mathbf{C}}$ is positive semi-definite. However, the matrix $\hat{\mathbf{C}}$ manifestly is not, as it possesses the negative eigenvalue $-(\frac{1}{l})^2\mathbf{n}_l \cdot \tilde{\mathbf{C}}\mathbf{n}_l$.

The $2 < l < n$ states, however, are in general not fixed points, except for very particular choices for the patterns of afferent activity.

In summary, the minimal multiplicative model is guaranteed to possess segregated fixed points, and these are guaranteed to be strictly stable provided that $C_{ii} > C_{ji} \, \forall i, j \neq i$. This condition is satisfied by ensembles that treat all the afferents in an unbiased manner. The minimal multiplicative model may also possess many unsegregated fixed points (potentially $2^n - n - 1$ of them), but the strict stability of the segregated fixed points guarantees that any such unsegregated fixed points are unstable.

2.2 General "Linear" Multiplicative Model

We now turn to a consideration of a wider class of multiplicative models, in which the functions Π, ρ and σ are unknown, but in which f and g are still the identity functions, so that the linear sum $\sum_i v_i = 1$ is maintained via the subtraction of a term $v_i A$ from the unconstrained growth rule. This is why we refer to this class of models as general "linear" multiplicative models. Our aim is to derive conditions on the functions Π, ρ and σ that guarantee that this class of models will exhibit the required fixed point structure. Our basic equation is then just

$$\dot{v}_i = \Pi(\mathbf{a} \cdot \mathbf{v}) \left[\pi(v_i, a_i) - v_i \sum_j \pi(v_j, a_j) \right], \tag{22}$$

where $\sum_i v_i = 1$ and, as usual, $\pi(v_i, a_i) = \rho(a_i)\sigma(v_i)$.

Consider, as before, the point $\mathbf{u}$ with components $u_j = \delta_{ij}$, i.e., a segregated state in which all afferents but afferent i have been eliminated. Expand about this point as before by writing $\mathbf{v} = \mathbf{u} + \delta\mathbf{v}$, where $\mathbf{n} \cdot \delta\mathbf{v} = 0$. For $\mathbf{u}$ to be a fixed point of the equations after ensemble averaging, we must have that

$$\sigma(0) \left\langle \Pi(a_i)\rho(a_j) \right\rangle = 0 \quad \forall j \neq i. \tag{23}$$

As the term in angle brackets is not guaranteed to be zero, we are forced to require that

$$\sigma(0) = 0. \tag{24}$$

This is the reason for our assuming separability of the function $\pi(v_i, a_i)$. With $\sigma(0) = 0$, after linearising we obtain, for $j \neq i$,

$$\delta\dot{v}_j = \delta v_j \Pi(a_i) \left[\sigma'(0)\rho(a_j) - \sigma(1)\rho(a_i)\right], \tag{25}$$

and the equation for $\delta\dot{v}_i$ can be obtained by using $\delta\dot{v}_i = -\sum_{j\neq i} \delta\dot{v}_j$. For the stability of this point, we require the ensemble average of the right-hand-side (RHS) to be non-positive. Thus, if

$$\sigma'(0) \leq \sigma(1) \tag{26}$$

and

$$\langle \Pi(a_i)\rho(a_j)\rangle \leq \langle \Pi(a_i)\rho(a_i)\rangle \quad \forall j \neq i, \tag{27}$$

then this segregated fixed point is guaranteed to be stable. A strict inequality in Eq.(27) will ensure strictly stable segregated fixed points and is required for the applicability of our results to the full, non-linear case. Defining the matrix $\mathbf{D}$ with components D_{ij} given by

$$D_{ij} = \langle \Pi(a_i)\rho(a_j)\rangle, \tag{28}$$

we must find conditions on the functions Π and ρ such that $D_{ii} > D_{ij}\ \forall i, j \neq i$. Notice that the matrix $\mathbf{D}$ is not, in general, symmetric. For the unbiased ensembles of afferent activity discussed above, we show in the Appendix that if Π and ρ are either both monotonic increasing or both monotonic decreasing, then this condition is satisfied.

We now consider the states corresponding to the unsegregated states defined by Eq. (15). For these states to be fixed points, we require that

$$\left\langle \Pi(\mathbf{a}\cdot\mathbf{u}) \left[\rho(a_i) - \frac{1}{l}\sum_{j=1}^{l} \rho(a_j) \right] \right\rangle = 0 \quad i \leq l. \tag{29}$$

With ρ a constant function, this condition is satisfied for any l, but we exclude this possibility because the pre-synaptic response function should depend on afferent activity. For $\Pi(x)$ and $\rho(x)$ both the identity function, the condition reduces to that for the minimal multiplicative model discussed above. Unless $l = n$, however, in general this condition is never satisfied for general functions Π and ρ except for very particular patterns of afferent activity. In particular, suppose that the ensemble consists exclusively of a set of non-singleton subensembles in which $\mathbf{a}\cdot\mathbf{u}$ is constant over a given subensemble. Then, for Eq. (29) to be satisfied, we require that, within each subensemble, $\langle \rho(a_i) \rangle = \langle \rho(a_j) \rangle \; \forall i, j \neq i$, and $i, j \leq l$. This requirement is met provided that that all pairs of afferents for $i \leq l$ are treated identically within the subensemble. For $l = n$ and unbiased activity patterns, it should be noted that these conditions are guaranteed to be satisfied, so that, for unbiased patterns, the $l = n$ state is always a fixed point. For $l < n$, a class of patterns that satisfies Eq. (29) is one generated from a basic pattern of afferent activity together with all its component permutations.

Define $\mu = \mathbf{a}\cdot\mathbf{u}$, let $\langle\rangle_\mu$ denote an average over the subensemble with $\mathbf{a}\cdot\mathbf{u} = \mu$, and let $\sum_\mu$ denote the sum over all such subensembles. Writing $\langle \rho(a_i) \rangle_\mu = \bar{\rho}_\mu$, a constant for $i \leq l$, we have that $\frac{1}{l}\sum_{j=1}^{l} \rho(a_j) = \bar{\rho}_\mu$ when $\mathbf{a}$ is in the subensemble with $\mathbf{a}\cdot\mathbf{u} = \mu$. Then, expanding about these points as usual by writing $\mathbf{v} = \mathbf{u} + \delta\mathbf{v}$ where $\mathbf{n}\cdot\delta\mathbf{v} = 0$, after some algebra and repeated use of $\sum_{j=1}^{l} \delta v_j = -\sum_{j=l+1}^{n} \delta v_j$, for $i \leq l$ we obtain

$$\begin{aligned} \delta\dot{v}_i &= \sigma\left(\frac{1}{l}\right)\sum_\mu \Pi'(\mu)\langle\rho(a_i)\mathbf{a}\rangle_\mu\cdot\delta\mathbf{v} \\ &+ \delta v_i\left[\sigma'\left(\frac{1}{l}\right) - l\,\sigma\left(\frac{1}{l}\right)\right]\sum_\mu \Pi(\mu)\bar{\rho}_\mu \\ &- \sigma\left(\frac{1}{l}\right)\sum_\mu \Pi'(\mu)\bar{\rho}_\mu\sum_{j=l+1}^{n}\langle a_j-\mu\rangle_\mu\delta v_j \\ &+ \frac{1}{l}\sum_\mu \Pi(\mu)\sum_{j=l+1}^{n}\left[\sigma'\left(\frac{1}{l}\right)\bar{\rho}_\mu - \sigma'(0)\langle\rho(a_j)\rangle_\mu\right]\delta v_j \end{aligned} \tag{30}$$

and for $i > l$ we have

$$\delta v_i = \delta v_i\sum_\mu \Pi(\mu)\left[\sigma'(0)\langle\rho(a_i)\rangle_\mu - l\,\sigma\left(\frac{1}{l}\right)\bar{\rho}_\mu\right] \tag{31}$$

as the linearised equations for the evolution of δv_i after ensemble averaging. $n-l$ of the eigenvalues of the matrix determining the linearised dynamics can be read off immediately, and the remaining l eigenvalues are given by the eigenvalues of the matrix $\hat{\mathbf{E}}$ with components $\hat{E}_{ij}$ given by

$$\hat{E}_{ij} = \sigma\left(\frac{1}{l}\right)\sum_\mu \Pi'(\mu)\langle\rho(a_i)a_j\rangle_\mu + \delta_{ij}\left[\sigma'\left(\frac{1}{l}\right) - l\,\sigma\left(\frac{1}{l}\right)\right]\sum_\mu \Pi(\mu)\,\bar{\rho}_\mu, \quad i,j\le l. \tag{32}$$

The matrix $\hat{\mathbf{E}}$ is not, in general, symmetric. However, as with $\hat{\mathbf{C}}$, it is easy to see that $\mathbf{n}_l$ is an eigenvector of $\hat{\mathbf{E}}$, and has eigenvalue

$$\lambda_1(\hat{\mathbf{E}}) = \sigma\left(\frac{1}{l}\right)l\sum_\mu \mu\,\Pi'(\mu)\bar{\rho}_\mu + \left[\sigma'\left(\frac{1}{l}\right) - l\,\sigma\left(\frac{1}{l}\right)\right]\sum_\mu \Pi(\mu)\,\bar{\rho}_\mu. \tag{33}$$

When $l = n$, $\mathbf{n}$ is an eigenvector of $\hat{\mathbf{E}}$, but $\mathbf{n}\cdot\delta\mathbf{v}\equiv 0$, so the sign of $\lambda_1(\hat{\mathbf{E}})$ is irrelevant to the stability analysis. However, we can prove the existence of another eigenvalue not associated with $\mathbf{n}_l$ that is positive, so that we do not need to consider the two cases $l = n$ and $l < n$ separately. Unlike $\hat{\mathbf{C}}$, we cannot characterise $\hat{\mathbf{E}}$'s other eigenvalues variationally. However, $\mathrm{Tr}\,\hat{\mathbf{E}} - \lambda_1(\hat{\mathbf{E}})$ gives the sum of the other eigenvalues, and if this sum is positive, then at least one positive eigenvalue of $\hat{\mathbf{E}}$ not associated with $\mathbf{n}_l$ must exist. We have that

$$\operatorname{Tr}\hat{\mathbf{E}} = \sigma\left(\frac{1}{l}\right)\sum_{\mu}\Pi'(\mu)\sum_{i=1}^{l}\langle\rho(a_i)a_i\rangle_{\mu} + l\left[\sigma'\left(\frac{1}{l}\right) - l\,\sigma\left(\frac{1}{l}\right)\right]\sum_{\mu}\Pi(\mu)\,\bar{\rho}_{\mu}, \qquad (34)$$

and so

$$\begin{aligned}\operatorname{Tr}\hat{\mathbf{E}} - \lambda_1(\hat{\mathbf{E}}) &= \sigma\left(\frac{1}{l}\right)\sum_{\mu}\Pi'(\mu)\sum_{i=1}^{l}\operatorname{Cov}(\rho(a_i), a_i)_{\mu} \\ &+ (l-1)\left[\sigma'\left(\frac{1}{l}\right) - l\,\sigma\left(\frac{1}{l}\right)\right]\sum_{\mu}\Pi(\mu)\,\bar{\rho}_{\mu}, \qquad (35)\end{aligned}$$

where $\operatorname{Cov}(\rho(a_i), a_i)_{\mu} = \langle[\rho(a_i) - \bar{\rho}_{\mu}][a_i - \mu]\rangle_{\mu}$. The second term on the RHS is positive if

$$\frac{1}{l}\sigma'\left(\frac{1}{l}\right) \geq \sigma\left(\frac{1}{l}\right) \quad 1 < l \leq n. \qquad (36)$$

If ρ is monotonic increasing (decreasing), then $\rho(a_i)$ and a_i, $i = 1, \ldots, l$, positively (negatively) co-vary. Thus, the first term on the RHS is positive if $\Pi'\rho' \geq 0$, the same condition that guarantees that the segregated fixed points are strictly stable. Clearly, these arguments go through for any non-singleton subset of afferents, not just the subset $i = 1, \ldots, l$. Hence, for Π and ρ either both monotonic increasing or both monotonic decreasing, and Eq. (36) satisfied, $\hat{\mathbf{E}}$ has a positive eigenvalue not associated with $\mathbf{n}_l$, and so any unsegregated fixed point states are all unstable.

For the general "linear" multiplicative model to exhibit the correct dynamics, corresponding to the presence of strictly stable, segregated fixed points and any unsegregated fixed points being unstable, we thus have derived a number of conditions on the functions Π, ρ and σ based on the assumption that all afferents are treated in an unbiased manner. To examine the stability of the unsegregated states, a stronger assumption was necessary. Without this stronger assumption, the unsegregated states are not, in fact, fixed points, except when $l = n$, in which case the stronger assumption reduces to the unbiased assumption. For the segregated points to be fixed points, we require that $\sigma(0) = 0$. In order to guarantee the strict stability of the segregated fixed points, we require that $\Pi'\rho' \geq 0$, i.e., Π and ρ must both be monotonic increasing or monotonic decreasing; and we must also have that $\sigma'(0) \leq \sigma(1)$. For any unsegregated fixed point to be unstable, in addition to needing $\Pi'\rho' \geq 0$, we must also have that $\frac{1}{n}\sigma'\left(\frac{1}{n}\right) \geq \sigma\left(\frac{1}{n}\right)$ for any positive integer n since we can have any number of afferents.

We can recast the various conditions on the function σ in a more intuitive manner. The sequence $\{\frac{1}{n} \mid n \in \mathbf{N}^+\}$ possesses an accumulation point at zero. We can therefore regard Eq. (36) as an equation in a continuous variable in the neighbourhood of zero. We then have the simple differential equation $\sigma'(x)/\sigma(x) \geq 1/x$, or $\sigma(x) \geq Ax$, where A is some positive constant. Eq. (36) therefore says that the function σ must grow at least as fast as linearly in its argument. Assuming that σ is monotonic increasing and extending $\sigma(x) \geq Ax$ over the whole interval $[0, 1]$, this condition then also implies that $\sigma'(0) \leq \sigma(1)$, which is necessary for the stability of the segregated fixed points. We should stress that we must be careful in the application of the condition $\sigma(x) \geq Ax$. For example, it is illegitimate to argue that the constant function $\sigma(x) = A$ satisfies this condition on the interval $[0, 1]$ and therefore should lead to acceptable dynamics. For, if σ is a non-zero constant, then $\sigma' = 0$, and Eq. (36) is violated for all positive n, and the requirement that $\sigma(0) = 0$ is also violated. The correct interpretation of $\sigma(x) \geq Ax$ is, rather, that σ grows at least as fast as linearly in its argument.

In summary, we can list the three derived conditions, and their origins, on the functions Π, ρ and σ:

1. $\sigma(0) = 0$ (segregated states are fixed points);

2. $\sigma(x) \geq Ax$ (instability of unsegregated fixed points);

3. $\Pi'(x)\rho'(x) \geq 0 \; \forall x$ (stability of segregated points).

These conditions guarantee that the general "linear" multiplicative model possesses the correct fixed point structure.

2.3 Fully General Model

Finally, we consider the fully general model in Eq. (6),

$$\dot{v}_i = \Pi(\mathbf{a} \cdot \mathbf{v}) \left[\pi(v_i, a_i) - g(v_i) \frac{\sum_j f'(v_j)\pi(v_j, a_j)}{\sum_j f'(v_j) g(v_j)} \right], \tag{37}$$

with $\sum_i f(v_i) = 1$, where f is some invertible function, and, as usual, $\pi(v_i, a_i) = \rho(a_i)\sigma(a_i)$. Although messier, the analysis of the fully general model is very similar to that of the general "linear" multiplicative model. We therefore do not labour the analysis, but rather state the key results. We continue to assume that the ensemble of afferent activity patterns treats all afferents in an unbiased manner.

Consider the segregated state $\mathbf{u}$, $u_j = \delta_{ij}$. We require that $f(1)+(n-1)f(0) = 1$. This must hold for any positive integer value for n, so we must have that $f(0) = 0$ and $f(1) = 1$. This segregated state is a fixed point of the full dynamics if

$$\sigma(0) = 0, \tag{38}$$

$$g(0) = 0. \tag{39}$$

Expanding about this point as usual, we obtain

$$\delta\dot{v}_j = \delta v_j \Pi(a_i) \left[\sigma'(0)\rho(a_j) - \sigma(1)\frac{g'(0)}{g(1)}\rho(a_i) \right] \tag{40}$$

as the linearised evolution equation for δv_j, $j \neq i$. As for the general "linear" multiplicative model, this point is therefore guaranteed strictly stable if Π and ρ are monotonic (either both increasing or both decreasing). However, the previous condition $\sigma'(0) \leq \sigma(1)$ becomes

$$\frac{\sigma'(0)}{\sigma(1)} \leq \frac{g'(0)}{g(1)}. \tag{41}$$

Now consider the unsegregated states $\mathbf{u}$ defined by $u_i = \gamma$, $i \leq l$, and $u_i = 0$, $i > l$, where $lf(\gamma) = 1$, so that $\gamma = f^{-1}(\frac{1}{l})$, this being the reason for assuming invertibility of f. As before, these states are fixed points if all afferents are treated in an unbiased manner and if the ensemble decomposes into subensembles in which $\mathbf{a} \cdot \mathbf{u}$ is constant. After some algebra, we obtain, for $i \leq l$

$$\begin{aligned}
\delta \dot{v}_i &= \sigma(\gamma) \sum_\mu \Pi'(\mu) \langle \rho(a_i) \mathbf{a} \rangle_\mu \cdot \delta \mathbf{v} \\
&+ \delta v_i \left[\sigma'(\gamma) - \sigma(\gamma) \frac{g'(\gamma)}{g(\gamma)} \right] \sum_\mu \Pi(\mu) \bar{\rho}_\mu \\
&- \sigma(\gamma) \sum_\mu \Pi'(\mu) \bar{\rho}_\mu \sum_{j=l+1}^{n} \left\langle a_j - \frac{\mu}{l\gamma} \right\rangle_\mu \delta v_j \\
&+ \frac{1}{lg(\gamma) f'(\gamma)} \sum_\mu \Pi(\mu) \sum_{j=l+1}^{n} \left[G \bar{\rho}_\mu - H \langle \rho(a_j)) _\mu \right] \delta v_j,
\end{aligned} \tag{42}$$

where

$$G = \sigma(\gamma) f'(0) g'(0) - f'(\gamma) \sigma(\gamma) g'(\gamma) + f'(\gamma) \sigma'(\gamma) g(\gamma), \tag{43}$$

$$H = g(\gamma) f'(0) \sigma'(0), \tag{44}$$

and for $i > l$ we have

$$\delta v_i = \delta v_i \sum_\mu \Pi(\mu) \left[\sigma'(0) \langle \rho(a_i)) _\mu - g'(0) \frac{\sigma(\gamma)}{g(\gamma)} \bar{\rho}_\mu \right] \tag{45}$$

as the linearised evolution equations for δv_i. As before, these points are unstable if $\Pi' \rho' \geq 0$. But, the condition in Eq. (36) for the general "linear" multiplicative model becomes

$$\frac{\sigma'(\gamma)}{\sigma(\gamma)} \geq \frac{g'(\gamma)}{g(\gamma)} \tag{46}$$

with $\gamma = f^{-1}(\frac{1}{l})$, $1 < l \leq n$. There can be any number of afferents, so this condition must hold for any positive n. As the sequence $\{f^{-1}(\frac{1}{n}) \mid n \in \mathbf{N}^+\}$ possesses an accumulation point at $f^{-1}(0) = 0$, we can, as before, regard this as an equation in a continuous variable in the neighbourhood of this point, and hence we have $\sigma'(x)/\sigma(x) \geq g'(x)/g(x)$, or $\sigma(x) \geq Ag(x)$, where A is some positive constant. Thus, σ must grow at least as fast as g, modulo an overall constant. As in the earlier discussion of Eq. (36) for the general "linear" multiplicative model, we must be careful in the application of $\sigma(x) \geq Ag(x)$. It is illegitimate, for example, to extremise the RHS of the inequality on the interval $[0, 1]$ and set σ to the constant function whose value is this extremum, for Eq. (46) would then be violated, as would the requirement that $\sigma(0) = 0$. Again, the correct interpretation is that σ grows at least as fast as the function g.

In contrast to the specific case $g(x) = x$ considered for the general "linear" multiplicative model, if σ and g are both monotonic increasing and we extend $\sigma(x) \geq Ag(x)$ over the whole interval $[0, 1]$, then this does not imply, in general, that Eq. (41) is automatically satisfied. However, when both σ and g are of the same functional form (e.g., both simple powers of their arguments, or both exponential functions of their arguments), then $\sigma(x) \geq Ag(x)$ does imply that Eq. (41) is satisfied.

In summary, assuming unbiased afferent activity patterns, the conditions on the functions Π, ρ, σ and g that guarantee that the fully general model exhibits the required fixed point dynamics are simply

1. $\sigma(0) = 0$, $g(0) = 0$;

2. $\sigma(x) \geq Ag(x)$;

3. $\Pi'(x)\rho'(x) \geq 0$.

There are no conditions on f, save that it is invertible, and that it satisfies $f(0) = 0$ and $f(1) = 1$.

2.4 Particular Models and Special Subclasses

We can employ our results from the above analyses to understand some of the particular models typically employed in the literature, and to examine some special subclasses of models in which elegant simplifications occur.

2.4.1 Standard Hebb Models

A standard Hebb model is almost always stated with a pre-synaptic function of the very restricted form $\pi(v_i, a_i) = a_i$, i.e., $\sigma(x) = 1$ and $\rho(x) = x$. Of course, $\sigma(x) = 1$ violates the requirement that $\sigma(0) = 0$, which guarantees that segregated states correspond to fixed points. Indeed, it is well know that the standard form of a Hebb model does not exhibit a fixed point structure. Nevertheless, the overall dynamics can still be understood by examining the linearised equations on the assumption that *ad hoc* devices such as freezing synapses at the minimum or maximum desired values will give fixed point-like behaviour, and thus our other criteria are applicable. Under multiplicative normalisation (von der Malsburg, 1973), $g(x) = x$. In this case, the condition in Eq. (46) is violated. Under subtractive normalisation (Goodhill & Barrow, 1994; Miller & MacKay, 1994), however, $g(x) = 1$. In this case, the condition in Eq. (46) is respected. Hence, we would expect multiplicative normalisation to fail, in general, to segregate afferents in a standard Hebb model. In fact, it is well known that while multiplicative normalisation can segregate anti-correlated afferents in a standard Hebb model, it cannot segregate positively correlated afferents. Our criteria apply if a model possesses a fixed point structure corresponding to the segregation of all but perfectly correlated afferents. As multiplicative normalisation in a standard Hebb model cannot segregate all but perfectly correlated afferents, our criteria correctly confirm its failure. In contrast, our criteria establish that subtractive normalisation in a standard Hebb model should be able to segregate all but positively correlated afferents, and this is indeed the case. Notice that these results are independent of the form of the function f, and, in particular, whether we enforce $\sum_i v_i = 1$ or $\sum_i v_i^2 = 1$.

2.4.2 Non-standard Hebb Models

If the pair of functions $(\sigma(x), g(x))$ define both the pre-synaptic response as a function of the number of synapses and the form of the term that enforces synaptic normalisation, then a standard Hebb model under multiplicative normalisation can be written as the $(1, x)$ model. The failure of the $(1, x)$ model in general to segregate afferents led to subtractive normalisation, which is the $(1, 1)$ model. One of our criteria for the capacity of a model to segregate all but perfectly correlated afferents is that $\sigma(x) \geq Ag(x)$, interpreted as meaning that $\sigma(x)$ must grow at least as fast as $g(x)$. Thus, rather than moving from the $(1, x)$ model to the $(1, 1)$ model, we can instead move to the (x, x) model. Provided that the other criteria are satisfied, the (x, x) model will segregate all but perfectly correlated afferents. Moreover, it satisfies the fixed point requirements $\sigma(0) = 0$, $g(0) = 0$, unlike the $(1, 1)$ model.

We have shown that our neurotrophic model of synaptic plasticity (Elliott & Shadbolt, 1998) can be reformulated as a non-linear Hebb model under multiplicative normalisation (Elliott & Shadbolt, 2002), where the non-linearity resides in the post-synaptic function Π. This model is precisely an (x, x) model. The neurotrophic model exhibits two distinct parameter regimes, one in which segregation of all but perfectly correlated afferents does occur, and one in which segregation never occurs. These two regimes were shown to correspond, respectively, to $\Pi' > 0$ and $\Pi' < 0$ ($\rho' > 0$ in both regimes). Hence, the criteria derived earlier give a more general understanding of our neurotrophic model by showing that the two distinct behaviours are not specific to the model but are, instead, universally valid: when the post-synaptic function Π is not monotonic increasing but ρ is monotonic increasing, the capacity for segregation breaks down.

For $n = 2$ afferents, the minimal multiplicative model, which is simplest (x, x) model, is identical to Swindale's model for the development of ocular dominance columns (Swindale, 1980). Let subscripted letter such as x and y denote different target cells, and let target cells be coupled through the lateral interaction function Δ_{xy}. Then the afferent input to target cell x is $c_x = \mathbf{a} \cdot \mathbf{v}_x$ and the full post-synaptic response can be written as

$$\Pi_x = \sum_y \Delta_{xy} c_y. \tag{47}$$

Defining $v_x = \frac{1}{2}(1 + v_{xi})$ for either of the two afferents i, and assuming that both afferents are treated in an unbiased manner so that $C_{11} = C_{22}$, we then obtain

$$\dot{v}_x = \frac{1}{2}(C_{11} - C_{12})(1 - v_x^2) \sum_y \Delta_{xy} v_y, \tag{48}$$

which, up to an overall multiplicative factor, is precisely Swindale's model. Thus, Swindale's model is formally identical to the minimal multiplicative model with $n = 2$ afferents.

2.4.3 The (x^a, x) Model with $a \leq 1$

We have just discussed the $(1, x)$ model, which is the standard Hebb model, and the (x, x) model, a non-standard Hebb model, both models employing multiplicative normalisation. The latter model possesses fixed points corresponding to the segregation all but perfectly correlated afferents, while the former can segregate only anti-correlated afferents. If we consider an "intermediate" model of the form (x^a, x), $0 \leq a \leq 1$, then as a approaches unity, we might expect this model to be able to segregate increasingly strongly correlated afferents. We now obtain a measure of the maximum strength of the correlations that this intermediate model can segregate. We assume that the model is minimal in all other respects, i.e., Π, ρ and f are all the identity functions. This model, after ensemble averaging, is then just

$$\dot{v}_i = \sigma(v_i)(\mathbf{C}\mathbf{v})_i - v_i\,\mathbf{v}^{\mathrm{T}}\mathbf{C}\boldsymbol{\sigma}, \tag{49}$$

where $\boldsymbol{\sigma} = (\sigma(v_1), \ldots, \sigma(v_n))^{\mathrm{T}}$, with $\sigma(x) = x^a$, and $C_{ij} = \langle a_i a_j \rangle$ as usual.

Although for $a \neq 0$, $\sigma(x) = x^a$ does satisfy $\sigma(0) = 0$, for $a < 1$, $\sigma'(0)$ is undefined, and hence the segregated states cannot be analysed simply. In our analyses above, we have found that the unsegregated states are always unstable if the segregated states are strictly stable. Because we cannot examine the stability of the segregated states, we now instead impose the existence of a completely unsegregated fixed point state (i.e., $l = n$) and determine when its stability reverses. Although the presence of a stable unsegregated state does not guarantee the presence of unstable segregated states, it does give an indication of when the dynamics of the model undergo qualitative change.

For simplicity, we consider just $n = 2$ afferents and expand about the unsegregated state by writing $v_i = \frac{1}{2} + \delta v_i$. Because $\delta v_1 = -\delta v_2$, we have only one independent equation, which, after linearisation, is

$$2^a \, \delta v_1 = \delta v_1 \left[a(C_{11} + C_{12}) - 2C_{12} \right], \tag{50}$$

where we have made the usual assumption that both afferents are treated in an unbiased manner, or $C_{11} = C_{22}$. The dynamics of the model change when

$$\frac{C_{12}}{C_{11}} = \frac{a}{2-a}. \tag{51}$$

Consider, for concreteness, the four binary activity vectors $(0,0)^{\mathrm{T}}$, $(0,1)^{\mathrm{T}}$, $(1,0)^{\mathrm{T}}$ and $(1,1)^{\mathrm{T}}$ occurring with probabilities $p/2$, $(1-p)/2$, $(1-p)/2$ and $p/2$, respectively. The parameter $p \in [0,1]$ is just the probability that the two afferents' activities are equal. Then the correlation matrix is simply

$$\mathbf{C} = \frac{1}{2} \begin{pmatrix} 1 & p \\ p & 1 \end{pmatrix}, \tag{52}$$

so that $C_{12}/C_{11} \equiv p$. Thus, for $p > a/(2-a)$, the unsegregated state is strictly stable, while for $p < a/(2-a)$, the unsegregated state is unstable. For the particular case $a = 0$, $p > 0$ guarantees stability, while for $a = 1$, $p < 1$ guarantees instability. For intermediate values of a, intermediate values of p are obtained. In particular, for $a = \frac{2}{3}$, the critical value of p is $\frac{1}{2}$. Hence, for $a > \frac{2}{3}$, the unsegregated fixed point starts to become unstable for values of p corresponding to positively correlated patterns of afferent activity, and so it may become possible to segregate such afferents.

2.4.4 Special Subclasses

The form of the general model in Eq. (6) is rather cumbersome, particularly the term

$$\frac{\sum_j f'(v_j)\pi(v_j, a_j)}{\sum_j f'(v_j) g(v_j)} \tag{53}$$

on the RHS. There are some subclasses in which this term simplifies, the simplest being the selection $f(x) = x$ and $g(x) = x$, this corresponding to the general "linear" multiplicative model discussed in detail earlier. In this case, the denominator collapses to unity, and we are left only with $\sum_j \pi(v_j, a_j)$.

If $f(x)$ is homogeneous of degree $a + 1$, then by Euler's theorem, $xf'(x) = (a + 1)f(x)$. Thus, if $g(x) = x$, then the denominator again collapses, as it becomes $\sum_j (a + 1)f(x_j) \equiv a + 1$, by definition. Of course, for a function of one variable, the only homogeneous function of degree $a + 1$ is $f(x) = x^{a+1}$ (and multiples thereof). In this case, Eq. (6) reduces to

$$\dot{v}_i = \Pi(\mathbf{a} \cdot \mathbf{v}) \left[\pi(v_i, a_i) - v_i \sum_j v_j^a \pi(v_j, a_j) \right]. \tag{54}$$

The general "linear" multiplicative model is the particular case $a = 0$.

3 Discussion

We have performed an analysis of a general class of Hebb growth rules under a general form of synaptic normalisation, characterised by Eq. (6), and extracted a set of conditions that guarantee that any particular model will exhibit the required fixed point structure characterising activity-dependent, competitive dynamics. That is, the conditions ensure the presence of strictly stable fixed points corresponding to segregated states in which all afferents but one have been eliminated, and when fixed points corresponding to unsegregated states in which two or more afferents innervate their target with equal strengths exist, these fixed points are unstable. These conditions, by construction, are independent of the size of afferent correlations, and are therefore valid for all but perfectly correlated afferents.

Other than the particular functional form of the rule in Eq. (6), our major assumption in deriving these conditions was that all afferents are treated in an unbiased manner. Such an assumption corresponds to the requirement that the ensemble of afferent activity patterns is translation invariant in the space of afferents, and is widely assumed in the modelling literature. Unbiased activity patterns correspond, for example, to normal patterns of vision during ocular dominance column development, in which afferents from either eye have a roughly equal chance of winning the competitive process. In contrast, biasing the patterns of activity towards one or more afferents would affect the fixed points and correspond to abnormal developmental processes such as ocular dominance column development under monocular deprivation, in which the closed eye has little chance of winning the competition. For biased inputs, it is to be expected that all segregated fixed points remain stable, but that the flow towards the segregated state in which the favoured input remains is more rapid than the flow towards the other segregated fixed points. If two or more inputs are equally favoured, then the same analysis as above would apply to competition between this subset of afferents. As we are interested here in normal developmental processes, we have restricted our analysis to unbiased afferent activity patterns.

We have implicitly assumed that the segregated and unsegregated fixed points entirely characterise the dynamics of the models analysed above. Such an assumption would be justified if the dynamics defined by Eq. (6) are curl-free, demonstrating the existence of a Lyapunov function and thus proving convergence to a stable state (Wiskott & Sejnowski, 1998). However, in general these dynamics are not curl-free, thus admitting of the possibility of limit cycles or oscillatory solutions. In general, it would be difficult to rule out such behaviour. However, numerical solutions of Eq. (6) for a range of possible models including the minimal multiplicative model show that these solutions are dominated by the fixed points analysed above and that convergence to the segregated fixed points always occurs (unpublished observations). While such observations are not conclusive, they do suggest that, for this class of models, oscillatory solutions are not present, or at least not generally observed.

We have analysed competitive dynamics on a pointwise basis only, at single target cells. Introducing multiple target cells coupled through lateral interactions generally renders such analyses very difficult if not intractable. Within the context of our earlier neurotrophic model (Elliott & Shadbolt, 1998), some analysis of coupled multiple target cells has been performed (unpublished observations). Introducing a lateral interaction function reduces the maximum size of afferent correlations below which afferent segregation is possible. This is a continuous process, so that this maximum size reduces continuously as a function of the lateral interaction strength. We expect similar results within the context of a general Hebb rule and a general form of synaptic normalisation. For only weak lateral interactions, we would expect to be able to continue to segregate strongly correlated afferents, although the maximum correlation value below which segregation is possible will be reduced a little below unity. As lateral interaction strength is increased, it should cease to be possible to segregate positively correlated afferents, with the segregation of only anti-correlated afferents being possible. For stronger lateral interactions still, afferent segregation should break down entirely.

For pointwise dynamics, provided that $\sigma(0) = 0$ and $g(0) = 0$, ensuring that segregated states are fixed points, and provided that $\sigma(x)$ grows at least as fast as $g(x)$, then the required competitive dynamics are guaranteed to be present in a model if $\Pi'(x)\rho'(x) \geq 0 \; \forall x$, i.e., if both Π and ρ are either monotonic increasing or monotonic decreasing. While the local dynamics of models may differ, their global dynamics, by construction, are identical. In the presence of multiple target cells and interactions between them, the global dynamics of a model determine the final structure of the resulting neuronal map, while the local dynamics determine how the model reaches that state. We may therefore regard all models in which Π and ρ are both monotonic increasing or both monotonic decreasing as equivalent and interchangeable, from a mathematical point of view. From a biological point of view, while the local dynamics of a model are important and can be used to resolve models by comparing their predictions against experiment, nevertheless, if, for example, two target cells possess differing but monotonic increasing post-synaptic response functions, then their responses are essentially equivalent, differing only in local detail. It is this equivalence that ensures that the global dynamics are identical. Mathematically, we are therefore justified in restricting attention to a consideration of the simplest and most natural form of monotonic Π and ρ, and these are arguably the forms $\Pi(x) = x$ and $\rho(x) = x$, the identity function in both cases.

This equivalence between models having monotonic increasing or monotonic decreasing Π and ρ raises issues about the evolvability and importance of activity-dependent, competitive dynamics in neuronal systems. Under the assumption that such neuronal dynamics have selective value and indeed have been a target for selection during evolution, it is natural to ask whether these dynamics are easy or difficult to evolve. From the analysis above, the resulting conditions that guarantee the presence of the required fixed point structure for all but perfectly correlated afferents are, in fact, rather easily satisfied. Thus, it would appear that evolution could satisfy these requirements without difficulty and that activity-dependent, neuronal competition should therefore be easily evolvable. But this argument is double-edged. For the relative ease with which these requirements may be satisfied raises the possibility that evolution satisfied them accidentally, and that activity-dependent, competitive neuronal dynamics have, or, at least, had no adaptive advantage. Certainly, the importance of the neuroanatomical structures to which neuronal competition characteristically gives rise has been questioned (Purves *et al.*, 1992), and we may broaden this questioning, in light of the ease with which our criteria may be satisfied, to ask whether activity-dependent, neuronal competition is itself important to the functioning of the vertebrate nervous system. Indeed, recent experimental data challenge the very existence of activity-dependent competition during developmental processes in some systems that hitherto have been regarded as archetypal examples of such dynamics (Crowley & Katz, 1999, 2000). Nevertheless, given the apparent ubiquity of activity-dependent, neuronal competition, it is tempting to dismiss this line of reasoning, but its very ubiquity may, rather, be an indication of the inevitability of the emergence of competition. Despite this, it remains a possibility that, even if activity-dependent, neuronal competition is an accidental discovery, it has subsequently been put to good use.

For multiplicative normalisation, for which $g(x) = x$, our criteria imply that, provided $\Pi'\rho' \geq 0$, it suffices to take $\sigma(x) = x^a$, $a \geq 1$, in order to guarantee that presence of the required fixed point structure for all but perfectly correlated afferents. Thus, the failure of multiplicative normalisation in a standard Hebb rule in which $\sigma(x) = 1$ is actually quite atypical. It thus seems odd that the possibility of expanding the standard Hebb rule to include a more general pre-synaptic term has evaded attention. We believe that the reason for this pivots centrally on interpretation. Most modellers have hitherto considered synaptic plasticity in an anatomically fixed network of variable-strength synapses. In contrast, our models have sought explicitly to address anatomical plasticity: the formation of new synapses and the removal of existing ones (Elliott & Shadbolt, 1998). In our models, the variable v_i denotes the (scaled) number of synapses between afferent i and its target, but in anatomically-fixed models it denotes synaptic efficacy (or strength or weight). In anatomically-fixed models, application of the Hebb rule gives the standard, well-known form, $\dot{v}_i = a_i \Pi$. In our models, however, we can regard the Hebb rule as a change per synapse, and therefore the total change in the number of synapses is given by the standard Hebb rule multiplied by the total number of synapses supported by an afferent: $\dot{v}_i = a_i v_i \Pi$. Thus, under an anatomical interpretation, we automatically have $\sigma(x) = x$, not $\sigma(x) = 1$. Indeed, this argument suggests that of all the possible forms for $\sigma(x)$ in the models considered above, the most natural choice, for a model of anatomical plasticity, is the linear form $\sigma(x) = x$. Given the linear form, the most natural choice for the normalising function $g(x)$ is then also the linear form $g(x) = x$, corresponding to multiplicative normalisation.

As noted earlier, Swindale's model of ocular dominance column formation (Swindale, 1980) is formally identical to the minimal multiplicative model with $n = 2$ afferents. Although Swindale introduced the term $1 - v_x^2$ in an *ad hoc* fashion, the equivalence shows that it can be derived formally and owes its origin to the underlying multiplicative normalisation. Oja's principal component analyser (Oja, 1982) is also very similar to the minimal multiplicative model, the only difference being that in the latter, a factor of v_i multiplies both the growth and the decay terms on the RHS, while in Oja's model, it is found only on the decay term. The models discussed here could be described as winner-take-all models at the afferent cell level. The conditions for winner-take-all dynamics at the target cell level have also been studied (e.g., Grossberg, 1987, 1988; Yuille, 1989).

In summary, we have performed an analysis of a general class of Hebb models under a general form of synaptic normalisation and extracted conditions that ensure that the models possess a fixed point structure allowing the segregation of all but perfectly correlated afferents. The resulting criteria are surprisingly easily satisfied, requiring that the pre- and post-synaptic functions ρ and Π are either both monotonic increasing or both monotonic decreasing, and that the function σ grows at least as fast as the function g. Competitive dynamics are therefore easily achieved in an infinite class of essentially equivalent models.

Appendix: Derivation of Conditions on Π and ρ

In Section 2.2 we defined the matrix $\mathbf{D}$ with components $D_{ij} = \langle \Pi(a_i)\rho(a_j) \rangle$ and, in order to guarantee the presence of strictly stable segregated fixed points, required that $\mathbf{D}$ satisfies $D_{ii} > D_{ij}$ $\forall i, j \neq i$. For ensembles of afferent activity that treat the afferents in an unbiased manner, we now derive conditions on the functions Π and ρ that guarantee that these strict inequalities are satisfied.

For ensemble element α, $\alpha = 1, \ldots, m$, define $\Pi_i^\alpha = \Pi(a_i^\alpha)$ and $\rho_i^\alpha = \rho(a_i^\alpha)$ and the corresponding m-dimensional vectors $\boldsymbol{\Pi}_i = (\Pi_i^1, \ldots, \Pi_i^m)^{\mathrm{T}}$ and $\boldsymbol{\rho}_i = (\rho_i^1, \ldots, \rho_i^m)^{\mathrm{T}}$ are vectors of functions of the activity of afferent i over the whole ensemble. Define, as before, $\mathbf{A}_i = (a_i^1, \ldots, a_i^m)^{\mathrm{T}}$. The requirement that $D_{ii} > D_{ij}$ $\forall i, j \neq i$ then becomes

$$\boldsymbol{\Pi}_i \cdot (\boldsymbol{\rho}_i - \boldsymbol{\rho}_j) > 0 \quad \forall i, j \neq i. \tag{55}$$

For ensembles that treat the afferents in an unbiased manner, the vectors $\mathbf{A}_i$ and $\mathbf{A}_j$ are related, as observed earlier, through a simple permutation of elements, so that $\mathbf{A}_j = \mathbf{R}\mathbf{A}_i$, where $\mathbf{R}$ is some permutation matrix, its characteristic feature being that on any row or column, there is precisely one entry of unity and zero elsewhere. Similarly $\boldsymbol{\Pi}_j = \mathbf{R}\boldsymbol{\Pi}_i$ and $\boldsymbol{\rho}_j = \mathbf{R}\boldsymbol{\rho}_i$. Thus, dropping the index i, and defining

$$\mathcal{E}_{\mathbf{R}} = \mathbf{\Pi} \cdot \boldsymbol{\rho} - \mathbf{\Pi} \cdot \mathbf{R}\boldsymbol{\rho}, \tag{56}$$

we require conditions on Π and ρ that guarantee that $\mathcal{E}_{\mathbf{R}} > 0 \ \forall \mathbf{R} \neq \mathbf{I}$.

We may assume, without loss of generality, that the components of $\mathbf{A}$, a^α, $\alpha = 1, \ldots, m$, are ordered so that $a^1 \geq a^2 \geq \ldots \geq a^m$. For suppose that $\tilde{\mathbf{A}}$ represents an unordered vector, with $\tilde{\mathbf{\Pi}}$ and $\tilde{\boldsymbol{\rho}}$ having components $\Pi(\tilde{a}^\alpha)$ and $\rho(\tilde{a}^\alpha)$, respectively. Let $\mathbf{A}$ represent an ordered vector, with the vectors $\mathbf{\Pi}$ and $\boldsymbol{\rho}$ defined as before. Let the matrix $\mathbf{R}_1$ be the permutation operator that orders the components of $\tilde{\mathbf{A}}$, so that $\mathbf{A} = \mathbf{R}_1\tilde{\mathbf{A}}$. Then

$$\begin{aligned} \tilde{\mathbf{\Pi}} \cdot \tilde{\boldsymbol{\rho}} - \tilde{\mathbf{\Pi}} \cdot \mathbf{R}\tilde{\boldsymbol{\rho}} &= \mathbf{\Pi} \cdot \mathbf{R}_1^{\mathrm{T}}\mathbf{R}_1\boldsymbol{\rho} - \mathbf{\Pi} \cdot \mathbf{R}_1^{\mathrm{T}}\mathbf{R}\mathbf{R}_1\boldsymbol{\rho} && (57) \\ &= \mathbf{\Pi} \cdot \boldsymbol{\rho} - \mathbf{\Pi} \cdot \mathbf{R}_2\boldsymbol{\rho}, && (58) \end{aligned}$$

since $\mathbf{R}_1^{\mathrm{T}}\mathbf{R}_1 = \mathbf{I}$ and $\mathbf{R}_2 = \mathbf{R}_1^{\mathrm{T}}\mathbf{R}\mathbf{R}_1$ is some other permutation operator. Thus, we may assume that the components of $\mathbf{A}$ are ordered without loss of generality provided that we can establish that $\mathcal{E}_{\mathbf{R}} > 0$ for all permutation matrices $\mathbf{R} \neq \mathbf{I}$.

Define the new variables $p^\alpha = \Pi^\alpha - \Pi^{\alpha+1}$, $r^\alpha = \rho^\alpha - \rho^{\alpha+1}$, $\alpha = 1, \ldots, m-1$, and $p^m = \sum_{\alpha=1}^m \Pi^\alpha$ and $r^m = \sum_{\alpha=1}^m \rho^\alpha$. The vectors $\mathbf{p} = (p^1, \ldots, p^m)^{\mathrm{T}}$ and $\mathbf{r} = (r^1, \ldots, r^m)^{\mathrm{T}}$ are related to the vectors $\mathbf{\Pi}$ and $\boldsymbol{\rho}$ through a matrix $\mathbf{T}$ by $\mathbf{p} = \mathbf{T}\mathbf{\Pi}$ and $\mathbf{r} = \mathbf{T}\boldsymbol{\rho}$, where $\mathbf{T}$ can be easily written down and has the inverse

$$\mathbf{T}^{-1} = \frac{1}{m} \begin{pmatrix} m-1 & m-2 & m-3 & \ldots & 2 & 1 & 1 \\ -1 & m-2 & m-3 & \ldots & 2 & 1 & 1 \\ -1 & -2 & m-3 & \ldots & 2 & 1 & 1 \\ -1 & -2 & -3 & \ldots & 2 & 1 & 1 \\ \vdots & \vdots & \vdots & & \vdots & \vdots & \vdots \\ -1 & -2 & -3 & \ldots & 2 & 1 & 1 \\ -1 & -2 & -3 & \ldots & -(m-2) & 1 & 1 \\ -1 & -2 & -3 & \ldots & -(m-2) & -(m-1) & 1 \end{pmatrix}. \tag{59}$$

Writing $\mathcal{E}_{\mathbf{R}} = \mathcal{E}_{\mathbf{R}}(\mathbf{\Pi}, \boldsymbol{\rho})$ instead in terms of these new variables, $\mathcal{E}_{\mathbf{R}} = \mathcal{E}_{\mathbf{R}}(\mathbf{p}, \mathbf{r})$, we can obtain the functional form of $\mathcal{E}_{\mathbf{R}} = \mathcal{E}_{\mathbf{R}}(\mathbf{p}, \mathbf{r})$ from $\mathcal{E}_{\mathbf{R}}(\mathbf{\Pi}, \boldsymbol{\rho})$. Because

$\mathcal{E}_{\mathbf{R}}$ is a product in the Π^α's and ρ^α's, it will similarly be a product in the p^α's and r^α's. Hence, we can write

$$\mathcal{E}_{\mathbf{R}} = \mathbf{p} \cdot \mathbf{S}\mathbf{r}, \tag{60}$$

where the elements of $\mathbf{S}$, $S_{\alpha\beta}$, are simply given by

$$S_{\alpha\beta} = \frac{\partial^2 \mathcal{E}_{\mathbf{R}}}{\partial p^\alpha \partial r^\beta}, \tag{61}$$

and these partial derivatives can be obtained from all the partial derivatives $\partial^2 \mathcal{E}_{\mathbf{R}} / \partial \Pi^\alpha \partial \rho^\beta$ by repeated application of the chain rule for partial differentiation using $\partial \Pi^\alpha / \partial p^\beta = \partial \rho^\alpha / \partial r^\beta = (\mathbf{T}^{-1})_{\alpha\beta}$.

For the permutation matrix $\mathbf{R}$, let the α^{th} row have an entry of unity in the s_α^{th} column and zero in all other columns. For $\mathbf{R}$ to be a permutation matrix, the set $\{s_1, \ldots, s_m\}$ must be a permutation of the set $\{1, \ldots, m\}$. Then we have that

$$\mathcal{E}_{\mathbf{R}} = \sum_{\alpha=1}^{m} \Pi^\alpha (\rho^\alpha - \rho^{s_\alpha}). \tag{62}$$

It is easy to see that $\partial \mathcal{E}_{\mathbf{R}} / \partial p^m = 0$ and $\partial \mathcal{E}_{\mathbf{R}} / \partial r^m = 0$, because $\sum_\alpha (\rho^\alpha - \rho^{s_\alpha}) \equiv 0$ and $\sum_\alpha (\Pi^\alpha - \Pi^{s_\alpha}) \equiv 0$. Hence, $\mathcal{E}_{\mathbf{R}}(\mathbf{p}, \mathbf{r})$ is independent of p^m and r^m, and so $S_{\alpha m} = 0 = S_{m\alpha}$ $\forall \alpha$. After some algebra, we can obtain the other partial derivatives in Eq. (61), to obtain, for $\alpha < m$ and $\beta < m$,

$$\frac{\partial^2 \mathcal{E}_{\mathbf{R}}}{\partial p^\alpha \partial r^\beta} = \min\{\alpha, \beta\} - \sum_{\mu=1}^{\alpha} \sum_{\nu=1}^{\beta} \delta_{\nu s_\mu}. \tag{63}$$

It is straightforward to see that $\sum_{\mu=1}^{\alpha} \sum_{\nu=1}^{\beta} \delta_{\nu s_\mu} \leq \min\{\alpha, \beta\}$ by considering the two cases $\alpha < \beta$ and $\alpha \geq \beta$ separately. Hence $\partial^2 \mathcal{E}_{\mathbf{R}} / \partial p^\alpha \partial r^\beta \geq 0$ $\forall \alpha, \beta$.

Pulling all this together, we may finally write $\mathcal{E}_{\mathbf{R}}$ in the form

$$\mathcal{E}_{\mathbf{R}} = \sum_{\alpha=1}^{m-1} \sum_{\beta=1}^{m-1} \left(\Pi^\alpha - \Pi^{\alpha+1}\right) \left[\min\{\alpha, \beta\} - \sum_{\mu=1}^{\alpha} \sum_{\nu=1}^{\beta} \delta_{\nu s_\mu}\right] \left(\rho^\beta - \rho^{\beta+1}\right), \tag{64}$$

where the term in square brackets on the RHS is non-negative. $\mathcal{E}_{\mathbf{R}}$ is therefore guaranteed positive if $(\Pi^\alpha - \Pi^{\alpha+1})(\rho^\beta - \rho^{\beta+1}) > 0$, $\forall \alpha < m$, $\forall \beta < m$. Thus, either both $\Pi^\alpha - \Pi^{\alpha+1}$ and $\rho^\beta - \rho^{\beta+1}$ are always positive, or both $\Pi^\alpha - \Pi^{\alpha+1}$ and $\rho^\beta - \rho^{\beta+1}$ are always negative. But the sequence $a^1, \ldots, a^m$ was assumed, without loss of generality, to be ordered, and therefore monotone. Hence, $\mathcal{E}_{\mathbf{R}}$ is guaranteed positive if the functions Π and ρ are either both monotonic increasing or both monotonic decreasing. Of course, Π or ρ a constant function forces $\mathcal{E}_{\mathbf{R}} = 0$, but we exclude this possibility by considering only non-constant Π and ρ.

A second, rather more direct geometric proof that $\mathcal{E}_{\mathbf{R}} > 0$ can be seen. If the functions Π and ρ are both monotonic increasing, and assuming without loss of generality that $a^1 \geq a^2 \geq \ldots \geq a^m$, then the vectors $\boldsymbol{\Pi}$ and $\boldsymbol{\rho}$ both lie in the m-dimensional infinite wedge defined by $x^1 \geq x^2 \geq \ldots \geq x^m \geq 0$, where the x^α are co-ordinates in m-dimensional Euclidean space. This wedge is constructed by taking the positive hyperquadrant defined by the hyperplanes $x^\alpha = 0$, $\forall \alpha$, and removing the regions corresponding to $x^\alpha < x^{\alpha+1}$, $\alpha = 1, \ldots, m-1$. Thus, the hyperplanes $x^\alpha = x^{\alpha+1}$, $\alpha = 1, \ldots, m-1$, contain the new faces of this region. Any permutation matrix $\mathbf{R}$ can be decomposed into a product of fundamental permutation matrices, these latter matrices simply exchanging only adjacent pairs of components. Thus, consider the matrix $\mathbf{R}^\alpha$, $\alpha = 1, \ldots, m-1$, that exchanges only the α^{th} and $(\alpha+1)^{\text{th}}$ components of a vector. $\mathbf{R}^\alpha$ acting on the vector $\boldsymbol{\rho}$ thus serves to reflect $\boldsymbol{\rho}$ in the hyperplane $x^\alpha = x^{\alpha+1}$ containing one of the faces of the wedge. Such an operation moves $\boldsymbol{\rho}$ out of the wedge by the same angle, relative to the hyperplane $x^\alpha = x^{\alpha+1}$, that $\boldsymbol{\rho}$ is within the wedge. Hence, $\boldsymbol{\Pi} \cdot \boldsymbol{\rho} > \boldsymbol{\Pi} \cdot \mathbf{R}^\alpha \boldsymbol{\rho}$. Repeated applications of further $\mathbf{R}^\alpha$'s continue to reflect $\boldsymbol{\rho}$ in these hyperplanes, either keeping it outside the wedge by the same angle relative to some hyperplane $x^\alpha = x^{\alpha+1}$, for some $\alpha < m$, that $\boldsymbol{\rho}$ is within the wedge, or returning it within the wedge necessarily back to $\boldsymbol{\rho}$. Hence, $\boldsymbol{\Pi} \cdot \boldsymbol{\rho} > \boldsymbol{\Pi} \cdot \mathbf{R}\boldsymbol{\rho}$ for any $\mathbf{R} \neq \mathbf{I}$, fundamental or otherwise. A similar argument applies if Π and ρ are both monotonic decreasing.

In addition to monotonicity of Π and ρ guaranteeing that $\mathcal{E}_{\mathbf{R}}$ is positive, setting $\Pi(x) = \rho(x)\ \forall x$ also achieves this. In this case, Π and ρ may be non-monotonic. However, the analysis of $\hat{\mathbf{E}}$ requires that Π and ρ are monotonic even if $\Pi = \rho$.

Acknowledgements: I thank the Royal Society for the support of a University Research Fellowship. I am indebted to the reviewers for providing many valuable suggestions for dramatically broadening the scope of the results derived here. I am especially grateful for the supplying of the variational proof for the existence of positive eigenvalues of symmetric matrices.

References

Bienenstock, E.L, Cooper, L.N., & Munro, P.W. (1982). Theory for the development of neuron selectivity: Orientation specificity and binocular interaction in visual cortex. *J. Neurosci.*, **2**, 32–48.

Crowley, J.C., & Katz, L.C. (1999). Development of ocular dominance columns in the absence of retinal input. *Nature Neurosci.*, **2**, 1125–1130.

Crowley, J.C., & Katz, L.C. (2000). Early development of ocular dominance columns. *Science*, **290**, 1321–1324.

Elliott, T., & Shadbolt, N.R. (1998). Competition for neurotrophic factors: Mathematical analysis. *Neural Comp.*, **10**, 1939–1981.

Elliott, T., & Shadbolt, N.R. (2002). Multiplicative synaptic normalisation and a non-linear Hebb rule underlie a neurotrophic model of competitive synaptic plasticity. *Neural Comp.*, **14**, 1311-1322.

Goodhill, G.J., & Barrow, H.G. (1994). The role of weight normalisation in competitive learning. *Neural Comp.*, **6**, 255–269.

Grossberg, S. (1987). Competitive learning: From interaction activation to adaptive resonance. *Cog. Sci.*, **11**, 23–63.

Grossberg, S. (1988). Nonlinear neural networks: Principles, mechanisms and architectures. *Neural Networks*, **1**, 17–61.

Harris, A.E., Ermentrout, G.B., & Small, S.L. (1997). A model of ocular dominance column development by competition for trophic support. *Proc. Natl. Acad. Sci. U.S.A.*, **94**, 9944–9949.

Hubel, D.H., & Wiesel, T.N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.*, **160**, 106–154.

Kohonen, T. (1995). *Self-Organizing Maps.* Heidelberg: Springer-Verlag.

McAllister, A.K., Katz, L.C., & Lo, D.C. (1999). Neurotrophins and synaptic plasticity. *Annu. Rev. Neurosci.*, **22**, 295–318.

Miller, K.D., & MacKay, D.J.C. (1994). The role of constraints in Hebbian learning. *Neural Comp.*, **6**, 100–126.

Oja, E. (1982). A simplified neuron model as a principal component analyzer. *J. Math. Biol.*, **15**, 267–273.

Purves, D., & Lichtman, J.W. (1985). *Principles of Neural Development.* Sunderland, MA: Sinauer.

Purves, D., Riddle, D.R., & LaMantia, A.-S. (1992). Iterated patterns of brain circuitry (or how the cortex gets its spots). *Trends Neurosci.*, **15**, 362–368.

Swindale, N.V. (1980). A model for the formation of ocular dominance stripes. *Proc. Roy. Soc. Lond. Ser. B*, **208**, 243–264.

von der Malsburg, C. (1973). Self–organization of orientation selective cells in the striate cortex. *Kybernetik*, **14**, 85–100.

von der Malsburg, C., & Willshaw, D.J. (1981). Differential equations for the development of topographical nerve fibre projections. *SIAM-AMS Proceedings*, **13**, 39–47.

Wiskott, L., & Sejnowski, T.J. (1998). Constrained optimization for neural map formation: A unifying framework for weight growth and normalization. *Neural Comp.*, **10**, 671–716.

Yuille, A.L. (1989). A winner-take-all mechanism based on presynaptic inhibition feedback. *Neural Comp.*, **1**, 334–347.