

Brain Stability and Neuron Connectivity

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In this paper we investigate the relationship between brain stability and the pattern of connections among the neurons composing the brain. We find that for a brain to be stable in the dynamic sense described below it must possess some crosswise or backward connections in addition to any forward connections it may possess. By implication, neural networks composed entirely of forward connections are not stable in the dynamic sense defined in this paper.

Introduction

In this paper we investigate the relationship between the pattern of interneuron connections in a brain, its topology, and the dynamic stability of the brain, a feature of its dynamics. We know that normal brains are stable in the sense that they do not spontaneously evolve toward coma or brain death on the one hand, or toward mania or seizure on the other. We also know that brains exhibit a pattern of connectivity, at least in part, that combines forward, backward, and cross connections between neurons. We shall show that the rich interconnectivity of brains is not accidental. Rather, it is necessary for brains to be dynamically stable in the sense just stated informally and defined precisely below.

Thus, effective brain function is not only a matter of adjusting synapse strengths to optimize some output, it is also a matter of providing a sufficiently rich pattern of neuron interconnectivity. In particular, as will be shown, a neural network with only forward connections between neurons can not be dynamically stable. For dynamic stability, a brain must possess some backward and/or cross connections.

In the following sections we begin by reviewing briefly the model of brain dynamics we shall use. Then we present a definition of dynamic brain stability and the conditions a brain must satisfy to be dynamically stable according to the definition. Next we define a partitioning of the set of neurons in the brain based on its connectivity. We use that partitioning to exhibit the form of the matrix of synapse weights for several patterns of connectivity. Finally, we demonstrate that the stability conditions cannot be satisfied if the weight matrix contains only forward connections.

Brain Model

Here we give a *brief* presentation of the mathematical model used to represent brains. A more detailed discussion may be found elsewhere [Ryon, 1997a]. See Kandel, *et al* for a thorough discussion of the neural science material.

We assume that the firing rate of neurons is the physical quantity of interest. We denote the firing rate of neuron i at time t by $r_i(t)$ and define it to be the average rate at which action potentials are initiated in the axon hillock of neuron i at time t . There is a time delay between the time an action potential fires in neuron i and the time it affects the firing of a successor neuron j . This time delay, denoted by t_{ij} , consists of the time required for an action potential to travel down the axon of neuron i , cross the synapse to neuron j , and diffuse along the dendrite tree and around the cell body to the hillock (trigger zone) of neuron j . Thus the firing rate of a neuron i is determined by the firing rates of the neurons that synapse upon it *at earlier times*.

The contribution neuron j makes to the membrane potential v_{ij} at the hillock of neuron i at time t is given by

$$v_{ij}(t) = w_{ij} r_j(t - t_{ji})$$

We take the potential to be a linear function of the firing rate r_j of neuron j at the earlier time t_{ji} . This means only that doubling the firing rate of neuron j at time $t - t_{ji}$ has the effect of doubling its contribution to the hillock membrane potential of the post synaptic neuron i at the later time t . The quantities w_{ij} are called the synapse weights or strengths. If neuron j does not synapse on neuron i then $w_{ij} = 0$.

The matrix $\mathbf{W} = [w_{ij}]$ determines the pattern of interconnection of the neurons in the brain. We sometimes say that \mathbf{W} represents the topology of the network.

The total membrane potential at the hillock of neuron i at time t is then the sum of the contributions from all its pre synaptic neurons.

$$v_i(t) = \sum_{j=1}^m v_{ij}(t) = \sum_{j=1}^m w_{ij} r_j(t - t_{ji})$$

Here m is the number of neurons in the brain.

The firing rate of neuron i at time t is determined by its hillock membrane potential

$$r_i(t) = \mathbf{s}(v_i(t)) = a_i \mathbf{s}_0 \left(x_1 + (v_i(t) - v_{i,\min}) \frac{\Delta x}{\Delta v_i} \right) = a_i \mathbf{s}_0 (s_i v_i(t) - \mathbf{q}_i)$$

where a_i is a constant, $\Delta v_i = v_{i,\max} - v_{i,\min}$ is the range of possible values of v_i , $\mathbf{s}_0(x)$ is the frequently used sigmoid function

$$s_0(x) = \frac{e^x}{1 + e^x}$$

and $\Delta x = x_2 - x_1$ is the *effective range* of the argument x of the sigmoid function $\sigma_0(x)$. Also, $s_i = \Delta x / \Delta v_i$ is a scale factor and $q_i = s_i v_{i,\min} - x_1$ is called the threshold, which is the value of the scaled potential at which the firing rate is at half maximum. The effective range, Δx , of the sigmoid argument x simply allows us to map the membrane potential range Δv_i onto any desired range of x values.

The above equation for $r_i(t)$ is an example of a more general one

$$r_i(t) = f_i(r_1(t - t_{1i}), r_2(t - t_{2i}), \dots, r_n(t - t_{ni}))$$

We refer to all such equations as *rate equations*.

A *solution* to these rate equations consists of functions $r_i(t)$ defined for all times in some non empty interval that satisfy the equations in the same time interval. We may also refer to solutions as *trajectories*.

Brain Stability

As suggested in the introduction, normal brains do not spontaneously evolve toward coma or brain death on the one hand, or toward mania or seizure on the other. We interpret coma and brain death to correspond to brain states in which the neuron firing rates are either repetitive or confined to very limited ranges of values such as zero, constant, or very weak. In dynamical systems such states are called fixed points (steady states), and limit cycles. We also interpret mania and seizure to correspond to brain states in which the firing rates approach their maximum possible values. In dynamical systems such trajectories are called unstable.

We require a definition of brain stability that is dynamic in that it corresponds to normal brain function. In our view, normal brains continuously evolve in a region of their state space that lies between the two extremes of steady state or limit cycles (coma or death) and hyperactivity (mania and seizure). Any concept of brain stability must accommodate this behavior.

In the mathematical theory of nonlinear dynamical systems, stability is often defined with respect to the steady states, and limit cycles. In the present context we regard steady states and limit cycles as *too stable* since they correspond to pathological brain states: coma or death. Instead, we adopt a modified form of Lyapunov stability [Lyapunov 1947]. Consider two brain states that are initially evolving in nearby trajectories. With time these two trajectories may converge to a single trajectory, diverge until they are greatly separated, or remain nearby for an appreciable length of time. If they converge, then the system is evolving toward a steady state. If they diverge, then the system is

evolving toward hyperactivity and is thus unstable. Finally, if they remain nearby as the systems continue to evolve, then the brain is stable in the dynamical sense we require.

We make this precise as follows: let $r_i(t)$ be a solution of the rate equations and let $s_i(t)$ be a nearby solution at time t . Then, following the conventional approach presented in many places [see Drazin 1994, Jackson 1995, Ott 1993, Saaty 1981, etc.], we write

$$s_i(t) = r_i(t) + \epsilon_i(t)$$

where the $\epsilon_i(t)$ are the small differences between the two solutions which we take to be of first order in smallness. If the following conditions hold

$$\Delta \epsilon_i(t) = \epsilon_i(t + \Delta t) - \epsilon_i(t) \cong 0$$

then the brain is stable. Here Δt is a time increment that is "large" in comparison to the time delays t_{ij} but "small" in comparison to the lifetime of the brain.

As we show in our companion paper [Ryon 1997b], by substituting the expression for $s_i(t)$ in the general rate equations given in the previous section and retaining only terms in first order, we obtain the linear equations

$$\epsilon_i(t + \delta t) = \sum_{k=1}^n f_{ik} \epsilon_k(t)$$

where δt is a time interval on the order of the average of the time delays t_{ij} and the f_{ij} are elements of the Jacobian matrix $\mathbf{F} = [f_{ij}]$ given by

$$f_{ij} = \frac{\partial r_i(t)}{\partial r_j} = a_i \frac{d\mathbf{s}_0(x)}{dx} \frac{\partial v_i(t)}{\partial r_j} \frac{\Delta x}{\Delta v_i} = a_i \frac{\Delta x}{\Delta v_i} \mathbf{s}'_0(x(v_i(t))) w_{ij} = b_i \mathbf{s}'_{0,i} w_{ij}$$

where $b_i = a_i \Delta x / \Delta v_i$ and $\mathbf{s}'_{0,i} = \mathbf{s}'_0(x(v_i(t)))$. The coefficients b_k and synapse strengths w_{ij} are constant over the short term. Thus any time dependence of \mathbf{F} comes from the factors $\mathbf{s}'_{0,k}$. We may also write

$$\mathbf{F} = [f_{ij}] = [b_i \mathbf{s}'_{0,i} w_{ij}]$$

If the magnitudes of all the $\epsilon_i(t)$ decreased with time, the nearby solutions would converge to a steady state or a limit cycle. If the magnitude of any one of them increased with time, the nearby solutions would diverge. In either case the brain state would become pathological.

Brain Stability Conditions

Let $\mathbf{u}^{[p]} = [u_i^p]$ be an eigenvector of \mathbf{F} with eigenvalue λ_p so that $\mathbf{F}\mathbf{u}^{[p]} = \lambda_p\mathbf{u}^{[p]}$. Since \mathbf{F} is real, its eigenvalues λ_p are either real or occur in complex conjugate pairs.

As we show in our companion paper [Ryon 1997b], by expanding $\mathbf{e}_i(t)$ in eigenvectors of \mathbf{F} , substituting into the linear equation for the time evolution of $\mathbf{e}_i(t)$, and iterating over k time intervals δt , we obtain the following equation for $\Delta\mathbf{e}_i(t)$:

$$\mathbf{e}_i(t + k\delta t) = \sum_{p=1}^m a_p (\mathbf{I}_p)^k u_i^p$$

where the a_p are the constant coefficients in the expansion.

It is clear from this last equation that the magnitudes of the $\mathbf{e}_i(t)$ will remain within given upper and lower bounds only if the following *conditions for brain stability* hold.

$$|\lambda_p| \cong 1$$

We see that if all λ_p satisfy $|\lambda_p| < 1$ then $\mathbf{e}_i(t)$ will decrease with time and the two solutions $r_i(t)$ and $s_i(t)$ will converge to a steady state or limit cycle. On the other hand, if any λ_p satisfies $|\lambda_p| > 1$ then $\mathbf{e}_i(t)$ will increase with time and $r_i(t)$ and $s_i(t)$ will diverge. Thus, to avoid convergence and divergence of trajectories, the stability conditions must hold.

It must be emphasized that the stability conditions are approximations and are only required to hold *on the average* for times long compared to δt but short compared to the lifetime of the system. A further discussion if this point is beyond the scope of this paper. Please see Ryon 1997b for details.

Neuron Connection Topology

Our demonstration depends on partitioning the neurons in a neural network in the following manner: Put into set S_0 all those neurons that have no incoming synapses. These are the sensory neurons that respond to non neuronal activity in the "outer" environment. Of the remaining neurons, put into set S_1 all those that receive synapses from neurons in S_0 . Of the remaining neurons, put into set S_2 all those that receive synapses from neurons in S_1 . Continue in this way until the set of remaining neurons is empty. Designate the last set of neurons formed by this process S_n . Finally, partition each set S_0, S_1, \dots, S_n into those that do not synapse upon subsequent neurons, the motor neurons, and those that do, the intermediate neurons. The result of this partitioning is shown in Figure 1.

The partitioning that results from this process is unique given a fixed specification of the neuron interconnections, say the weight matrix w_{ij} , and provided that there is at least one sensory neuron with no incoming synapses. If there are no sensory neurons then the network necessarily has backward or crosswise connections.

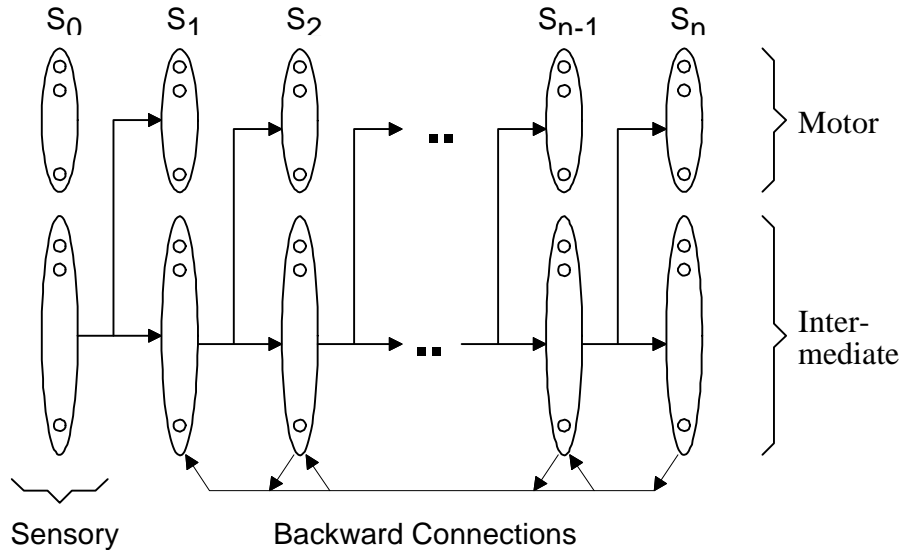


Figure 1. Partitioning a set of connected neurons into disjoint subsets based on distance from the set S_0 of sensory neurons. Sensory neurons are those without incoming synapses. Motor neurons are those without outgoing synapses. The logically possible set of sensory-motor neurons is physiologically unlikely.

We say the neurons in set S_1 are a distance 1 from those in S_0 , those in S_2 are a distance 2 from those in S_0 , and so on. Observe that motor neurons may be found at any distance from the sensory neurons, S_0 . Note also that logically a neuron may be both sensory and motor, a condition that is not known in nature.

Figure 1 also shows possible backward connections from neurons at greater distances from S_0 to those at lesser distances. By construction, there are no backward connections to set S_0 . Cross connections are not shown, but are understood to connect neurons within any set S_i . Also not shown are backward connections to motor neurons, which are possible but are omitted for simplicity.

We must emphasize that our partitioning is *logical only*. We make no claim that it corresponds to any natural brain organization.

The Matrix of Synapse Weights

The matrix or synapse weights or strengths is given by.

$$\mathbf{W} = \begin{bmatrix} W_{11} & W_{12} & \cdots & W_{1m} \\ W_{21} & W_{22} & \cdots & W_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ W_{m1} & W_{m2} & \cdots & W_{mm} \end{bmatrix}$$

where m is the total number of neurons.

We number the neurons such that neurons 1 through i belong to S_0 , neurons $i+1$ through j belong to S_1 , ..., neurons $k+1$ through m belong to S_n . The weight matrix may then be written in partitioned form as follows:

$$\mathbf{W} = \begin{bmatrix} W_{00} & W_{01} & \cdots & W_{0n} \\ W_{10} & W_{11} & \cdots & W_{1n} \\ \vdots & \vdots & \ddots & \vdots \\ W_{n0} & W_{n1} & \cdots & W_{nn} \end{bmatrix}$$

where W_{ij} is the submatrix of weights for synapses of neurons in S_j upon neurons in S_i . The diagonal submatrices contain the weights for all the *cross* connections in the network. The submatrices in the upper triangle contain weights for the *backward* connections. The submatrices in the lower triangle contain weights for the *forward* connections.

Case 1: Unrestricted Connections

By construction, the only non zero forward connections are between S_i and S_{i+1} . Thus all the submatrices in the upper triangle vanish except those immediately above the main diagonal. Furthermore, also by construction, there are no backward connections to neurons in S_0 . The weight matrix thus takes the following form:

$$\mathbf{W} = \begin{bmatrix} W_{00} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ W_{10} & W_{11} & \cdots & W_{1,n-2} & W_{1,n-1} & W_{1n} \\ \mathbf{0} & W_{21} & \cdots & W_{2,n-2} & W_{2,n-1} & W_{2n} \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & W_{n-1,n-2} & W_{n-1,n-1} & W_{n-1,n} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & W_{n,n-1} & W_{nn} \end{bmatrix}$$

Case 2: No Backward Connections

If we eliminate all backward connections the weight matrix becomes

$$\mathbf{W} = \begin{bmatrix} W_{00} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ W_{10} & W_{11} & \cdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & W_{21} & \cdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & W_{n-1,n-2} & W_{n-1,n-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & W_{n,n-1} & W_{nn} \end{bmatrix}$$

Note that the submatrices in the upper triangle all vanish.

Case 3: Forward Connections Only

If we eliminate both the backward and cross connections, leaving only the forward connections, the weight matrix becomes

$$\mathbf{W} = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ W_{10} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & W_{21} & \cdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & W_{n-1,n-2} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & W_{n,n-1} & \mathbf{0} \end{bmatrix}$$

Here, the only non-vanishing submatrices are those immediately below the main diagonal.

Connection Pattern and Brain Stability

We are now able to combine our observations and results of the previous sections and draw conclusions about the relationship between brain stability and neuron connectivity.

The conditions for brain stability are

$$|\lambda_p| \cong 1.$$

where the λ_p are the eigenvalues of the Jacobian matrix \mathbf{F} .

In Case 3 above, in which there are only forward connections, the weight matrix \mathbf{W} has the strictly lower triangular form

$$\mathbf{W} = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} \\ W_{10} & \mathbf{0} & \cdots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} \end{bmatrix}$$

in which only the submatrices immediately below the main diagonal are non zero. It follows that the Jacobian matrix \mathbf{F} has the same strictly lower triangular form

$$\mathbf{F} = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} \\ F_{10} & \mathbf{0} & \cdots & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} \end{bmatrix}$$

where the elements of each F_{pq} are given by

$$(F_{pq})_{ij} = b_i \mathbf{s}'_{0i} (W_{pq})_{ij}$$

In the Appendix we show that a real matrix in lower diagonal form

$$\mathbf{M} = \begin{bmatrix} \mathbf{m}_1 & 0 & \cdots & 0 \\ m_{21} & \mathbf{m}_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ m_{n1} & m_{n2} & \cdots & \mathbf{m}_n \end{bmatrix}$$

has eigenvalues $\mathbf{m}_1, \mathbf{m}_2, \dots, \mathbf{m}_n$. Thus it is clear that the eigenvalues of \mathbf{F} all vanish.

$$\lambda_p = 0 \text{ for all } p.$$

Consequently, the conditions for brain stability *cannot be satisfied* in this case. In fact, if the eigenvalues of \mathbf{F} all vanish, the equations given above for the difference between two nearby trajectories reduce to

$$\mathbf{e}_i(t + kd t) = 0$$

which imply that the two trajectories converge within δt to either a steady state or a cycle.

We restate the result for emphasis.

If a neural network contains only forward connections, then it cannot satisfy the stability conditions $|\lambda_p| \cong 1$.

This may also be put in a more positive form.

A necessary condition for a neural network to satisfy the stability conditions $|\lambda_p| \cong 1$ is that it contain some backward and/or crosswise connections.

On the other hand, in Cases 1 and 2 above \mathbf{W} , and thus \mathbf{F} , do not have strictly triangular form. Therefore the eigenvalues of \mathbf{F} *might not* all vanish and so the stability conditions *may be satisfied* depending on the specific values in the model at time t .

Conclusions

We have shown that a concept of dynamic stability for brains coupled with a partitioning of the weight matrix based on neuron connectivity leads to the conclusion that neural networks with only forward connections cannot be dynamically stable. Conversely, a dynamically stable neural network must have some backward and crosswise connections.

This result is consistent with our understanding of natural brains, at least those of higher organisms. For example, backward connections are known to be extensive in the cerebral cortex. Burnod has discussed the bidirectional connections in the entire cortex and represented them in a diagram showing remarkable symmetry [Burnod 1989]. Felleman and Van Essen have concentrated on the visual cortex and related areas of primates and produced a diagram showing extensive bidirectional connections between these numerous cortical areas [Felleman and Van Essen, 1991]. In addition, backwards connections may be found within a single cortical area. Kandel, Schwartz and Jessell discuss the primary visual cortex and present a diagram that shows forward connections from layer 4 to layers 2 and 3, from there to layer 5, then to layer 6, and finally *backwards* connections to layer 4 [Kandel, Schwartz and Jessell, 1995]. Their diagram also shows various types of crosswise connections within the primary visual cortex.

We are now in a position to understand that these backwards and crosswise connections are necessary for brains to be dynamically stable. We must also understand that backwards and crosswise connections are not sufficient to guarantee that the brains are stable. For that, one must verify that the stability conditions ($|\lambda_p| \cong 1$) are in fact satisfied, which is the subject of another paper.

We must emphasize that the concept of stability presented here does *not* entail an unvarying or static brain state. Stability is dynamic and perhaps is best understood as an approximate balance, over time, of tendencies for the system to evolve toward a steady state on the one hand and toward hyperactivity on the other. It is similar to the physicist's concept of dynamic equilibrium in thermodynamics. The concept is broad enough to encompass the full range of normal brain function. Brain stability is a dynamic balancing act and at any instant in time the brain may be found at some distance from the point of balance. What matters is that, over time, the brain remains within the region of its state space between hypoactivity (coma and brain death) and hyperactivity (mania and seizure).

Appendix

Here we show that the eigenvalues of a square matrix in lower diagonal form are its diagonal elements. Let \mathbf{M} be the lower diagonal matrix

$$\mathbf{M} = \begin{bmatrix} \mathbf{m}_1 & 0 & \cdots & 0 \\ m_{21} & \mathbf{m}_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ m_{n1} & m_{n2} & \cdots & \mathbf{m}_n \end{bmatrix}$$

The eigenvalues of \mathbf{M} are the roots of its characteristic polynomial

$$0 = |\mathbf{M} - \mathbf{mI}_n| = \begin{vmatrix} \mathbf{m}_1 - \mathbf{m} & 0 & \cdots & 0 \\ m_{21} & \mathbf{m}_2 - \mathbf{m} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ m_{n1} & m_{n2} & \cdots & \mathbf{m}_n - \mathbf{m} \end{vmatrix}$$

Expand the determinant by its first row

$$0 = |\mathbf{M} - \mathbf{mI}_n| = (\mathbf{m}_1 - \mathbf{m}) \begin{vmatrix} \mathbf{m}_2 - \mathbf{m} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ m_{n2} & \cdots & \mathbf{m}_n - \mathbf{m} \end{vmatrix}$$

Expand a second time.

$$0 = |\mathbf{M} - \mathbf{mI}_n| = (\mathbf{m}_1 - \mathbf{m})(\mathbf{m}_2 - \mathbf{m}) \begin{vmatrix} \mathbf{m}_3 - \mathbf{m} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ m_{n3} & \cdots & \mathbf{m}_n - \mathbf{m} \end{vmatrix}$$

Continue until

$$0 = |\mathbf{M} - \mathbf{mI}_n| = (\mathbf{m}_1 - \mathbf{m})(\mathbf{m}_2 - \mathbf{m}) \cdots (\mathbf{m}_n - \mathbf{m})$$

If the diagonal elements of \mathbf{M} all vanish the equation becomes

$$0 = |\mathbf{M} - \mathbf{mI}_n| = (-\mathbf{m})^n$$

Now it is clear that the roots of the characteristic polynomial are the diagonal elements $\mathbf{m}_1, \mathbf{m}_2, \dots, \mathbf{m}_n$ and that they are also the eigenvalues of the matrix. This result holds even when the diagonal elements all vanish.

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