Optimization in Structure and Function of the Brain; A Model for Synaptic Plasticity

Robert Englman

aSoreq NRC, Yavne 81800, Israel

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Abstract

A physicist’s point of view is presented of some of the expectations of neurobiologists regarding the criteria for the brain’s structure, which the brain needs to optimize for its efficient functioning. We have pointed out several lacunae in these criteria, notably in the meaning of the “economies” that are associated with the brain.

We have also constructed a model for synaptic plasticity or adaptibility, based on the Hebb-Hopfield stochastic formalization of neuron firing, which quantifies the enhanced range of firing (recognition) probabilities by the post-synaptic neuron after a previous presentation of a given pattern.

Dedicated to my grand-son Ori, the working of whose mind boggles my own.

A Quotation:

“The more we learn about the structure and function of the brain, the more we come to appreciate the great precision of... [its] construction and the efficiency of... [its] operation.” [1]

1 Economies...

About a century ago Ramon y Cajal postulated that the structure of the brain is the outcome of economies (or optimization or efficiency) in time, space and of the material of which the brain is composed. By “material” one is allowed to understand the neurons and the connections between them:
axons, synapses and dendrites. In a network picture of the brain, articulated in terms of "nodes" (neurons) and "edges" or "wires" (representing the connections between the neurons), the economy in materials is frequently expressed as "minimalization of wiring costs". A computational study performed on the observed locations and connections between 279 neurons in the minuscule worm *C. (Caenorhabditis) elegans* purported to show that indeed the "wiring costs" are approximately minimal for the actual arrangements [2]. [Oddly, the minimalization of neuronic material has not received attention. Nevertheless, it was noted that "...dendrites might control cell partitioning" ([3] Section 59). Also, Fig. 8 of that reference, captioned: "Perturbing cell dendrites disrupts cell mosaics", shows the interaction between neuron arrangement and dendrites in Ganglion cell layer (GCL) that contain dendrites and from which axons emanate to the brain. Still, to my knowledge, a combined dendrite and neuron location optimization study in the human brain has not been done in the general literature. An exception is the combined maximum entropy approach for these two variables by the present author [4]. Also, somewhat surprisingly, the "wiring cost" in [2] is reckoned as a quadratic, rather than a linear, function of the lengths of the wires.]

"Economy in time" in the Cajal picture may be understood as referring to either the the time needed for the development (mainly in the embryonic stage) of the brain network, or to the time involved in passing information across and inside the brain during its functioning. Further, "economy in space" relates to the available volume in the head (or parts of it), essentially of linear dimensions of 10 cm for humans, into which the brain has to be fitted.

The above three Cajal economy requirements have been subsequently enlarged in various respects, as follows:

First, by economy for "functionality" a concept widely held and noted [5], but only sparsely discussed or defined. It might mean, though, that minimalization of the wiring cost might be set aside in favor of a smooth working efficiency (possibly, error correction or adaptability, of which later).

Next comes energy economics [6], meaning the energy needed for brain processes (including the substantial energy amount for the resting, not functioning, brain) derived from oxygen and glucose consumption. This will include the energy uptake by the axons and the neurons alike, as well as the changes in the synaptic strengths, which accompany any active brain process.

Lastly, there is the requirement that the brain structure possess adaptability (or "brain plasticity"), meaning that it can (will) incorporate in its
structure any new information passed though it. In the commonly quoted Hebb and Hopfield pictures for learning this means that synaptic strengths will increase after each persistent brain activity. More recently, this requirement was interpreted in terms of the physical concept, namely that the network operates in a state of criticality. Notably, "criticality" is a physical situation where a transition between phases takes place (like from a liquid to a vapor phase), in which situation the system is subject to large fluctuations. This means that its micro-state scans a large number of state-varieties without energy intake or loss. Similarly, it is argued that the brain being purportedly in a "critical" state is capable of assuming many energetically adjacent configurations, thus having the quality of plasticity or adaptability. How the brain stabilizes in a new configuration (if it is not further stimulated) and how it can pass from this to a yet newer situation upon another novel stimulation, are one of the many unanswered questions of brain dynamics. Here I might quote an authoritative work: "[The minimization of the amount of wires to achieve small world configuration] assumes that "broadcasting" [=letting known of the nodes', neurons' existence] and routing information [= of the wires coming from the neuron] are known to each node. How this can be achieved - [namely] what aspects of the neural code convey its own routing information - remains an open question in neuroscience" [7].

Returning now to the term "economy", used repeatedly in the foregoing, this can have two different meanings, as it can also have in common, day-to-day parlance. It can mean "the least expending", as in "an economy car" that consumes, expends the least (or less than otherwise) gas for a given mileage. However, it can also mean that for a certain given expense it gives the greatest yield. For the car analogue the second meaning is actually identical to the first, since the car that consumes the least gas for the given mileage is also the car that give the largest mileage for a given quantity of gas. But the two meanings differ for an economizing household, since there by the first meaning an economizing or parsimonious family puts away after each month a certain amount of savings, whereas by the second meaning the family uses up its fixed amount of income fully, but does so in the most sensible way, by buying things lavishly but with choice of the cheapest alternatives.

The distinction is evident in the several requirements for brain structure mentioned above, for example that for economizing in space. Does this mean that that the size of the brain is given, fixed, e.g., by an upper limit on the skull size at birth as it emerges from the womb, and the evolving brain structure is the most economic, in the sense of its efficiency, given the limits
on its size? Or does "economy of size" mean that consistent with the needs of a fully functioning brain, the actual structure of the brain has minimal size?

I am delving on this point to show the ambiguity of the current use of the term "economy", or "parsimony", or "maximum efficiency" in the brain structure context, since the resolution of this ambiguity will be important in our formal optimization theory of the brain structure, later in this paper.

The following quantitative example is instructive and (at least) amusing: It is well known in Statistical Mechanics that one can derive the Gibbs-Boltzmann distribution among states with energies $E_i, (i = 1 - N)$, namely, the probability of state occupancy having the form (with the assumption of no energy degeneracy)

$$p_i \propto e^{-E_i/k_B T}, \quad k_B = \text{Boltzmann constant}, \quad T = \text{temperature} \quad (1)$$

from a maximalization of the entropy plus a mean energy term whose value is fixed by the relation $(1/k_B T) \sum_i p_i E_i = \text{a constant}$ (fixed by the normalization of the probabilities). The functional to be maximized has the form

$$H_S = -\sum p_i \ln p_i - \beta \sum p_i E_i \quad (2)$$

where $\beta$ is a Lagrange multiplier. Requiring $\frac{\partial H_S}{\partial p_i} = 0$ for all $i$ and setting $\beta = 1/(k_B T)$, so as to satisfy the fixed mean energy condition, gives (in the dense energy states limit) indeed equation (1), as formulated.

On the other hand, one can also minimize the mean energy subject to a fixed entropy value $-\sum p_i \ln p_i = \text{a constant}$, by minimizing the functional

$$H_E = \sum p_i E_i + \left(1/\beta'\right) \sum p_i \ln p_i \quad (3)$$

Here $1/\beta'$ is another Lagrange multiplier. Again, requiring $\frac{\partial H_E}{\partial p_i} = 0$ for all $i$ and setting $\beta' = 1/(k_B T)$, so as to satisfy the fixed entropy condition, gives indeed the probability distribution, as formulated in equation (1).

In this example (indicated to me a long time ago by Prof. R.D. Levine), the two meanings of "economy" ("cost" fixed and system’s efficiency or functionality optimized versus variable "cost" minimized and system’s performance fixed) are interchangeably ascribed to the mean energy and to the system’s entropy.

In summary, whereas it makes good sense to claim or to postulate that the existing brain (human or otherwise) has the property (properties) of economy, it is not clear from the literature in which of the two senses of
"economy" is the term used, 1) the most efficient utilization of a fixed "given", or 2) the most parsimonious arrangement for the brain, such that it has to perform a given set of tasks. This ambiguity may be one of the "open questions" in neurobiology, for which we have made the above citation.

2 What are the effective brain parameters?

The brain evolves and it has been empirically determined that at least one type of evolution of the normal, adult brain undergoes rapid changes under simulation in the time interval of between 0.015 and 0.06 seconds (or during about some tens of milliseconds) [8]. (Other long term changes are from the embryonic-to-adult stages and during senescence.) Despite the myriad of short term changes, the brain remains the brain and functions (more or less) effectively as such. So, in order to have an understanding of the brain structure, the individual neuron and axon arrangements need not be known or fixed. Equivalently, in terms of graph-theory (which is frequently used for the modelling of brain structure), one does not have to possess a full knowledge of all the axon-neuron connections (the adjacency matrix elements $w_{ij}$ in the Hebb-Hopfield formalisms) to know what is going on the functioning brain.

What then are the parameters which are necessary for a characterization of a functional brain?

Or, in terms of the six economy requirements with which we have started our discussion (economies in time, space, material, energy, functionality and adaptability), what are the parameters with respect to which the brain’s "cost function" has to be optimized (minimized), so as to characterize the brain? Unfortunately, the literature is silent on this point, though many interesting and useful characterization (for humans and otherwise) have appeared, but all these without pointing out their centrality to functioning. (Instead, they appeared to stress the similarity of the observed cerebral system to some model network, such as a "small world"-type of network.)

Some "global" parameter, such as the "clustering coefficient" (or "the average number of actual nearest neighbor links over the average number of such possible links", which has the value of about 0.28 in some brains [9]-[10]), or the frequency of some special motifs or loops [11] may play a role in the efficient functioning of human brain and their optimization may answer for the several economy requirements listed by us above. However, the mechanism through which they contribute to the achievement of an economy is not clear at this moment.
3 Learning, Synaptic Plasticity

The prevalent paradigm for the brain network activity is that a set of neurons "fire" (transmit electric impulses or charged ions) along a number of "axons" towards various near or distant neurons, with the transmissions entering the latter through synapses (gates) attached to the dendrites (tree-like protrusions) of the accepting neurons. These will "fire"-on to other neurons provided the incoming electric message reaches certain threshold value. In case of successful firing the two neurons (called the "pre-synaptic" and "post-synaptic" neurons) turn to the task of changing their intervening synapse’s strength, "learning" it so as to recognize (either immediately or after some further similar transmissions) messages identical or largely similar to the received previously and to transmit these further. This, then, is the basis for the network's learning capability, embodied in the plasticity (adaptability) of the synapses.

3.1 Illustration of learning

We suppose that the transmission coefficient $K_{ij}(t_0)$ of the signal between a pre-synaptic neuron $j$ and a post-synaptic neuron $i$, at the beginning of the time $t = t_0$ of brain activity takes only two possible values, namely $(+1, -1)$. (Similar assumptions have been made since the inception of brain network theory. The time index will be frequently omitted in the future.) Based on the picture of brain activity as sketched above, which has strong support from theory and physiological experiments, the quantity $K_{ij}$ is known as the synaptic strength. The message from the $j$-th neuron is denoted by $x_j$ and represents its electrical potential. We now suppose that the post-synaptic neuron’s potential, denoted by $h_i$, is the following weighted average of the contributions from N pre-synaptic neurons which communicate with it:

$$h_i(t) = \frac{1}{N} \sum_{i=1}^{N} K_{ij}(t)x_j(t)$$

(4)

For firing at a post-synaptic neuron, we require that

$$h_i > 0$$

(5)

(or, as discussed in more generality in the next section, some positive fraction.) In the following illustrative exercise we take for concreteness $N = 6$ and posit the following set of $j$-indexed values in the initial synaptic strength at neuron $i$

$$K_{ij}(t_0) = [-1, 1, -1, 1, -1, 1]$$

(6)
We next suppose a set of three elementary starting patterns
\[ x_j(t_0) = x_j^\mu(t_0), \quad \mu = 1 - 3 \] (7)
specified as
\begin{align*}
x_1^1(t_0) &= [1, 1, 1, 1, -1, -1] \\
x_2^2(t_0) &= [1, 1, -1, -1, 1, 1] \\
x_3^3(t_0) &= [-1, 1, 1, -1, -1]
\end{align*} (8)
Clearly, the patterns \( \mu = 1 \) and \( \mu = 2 \) presented at neurons \( i \) do not satisfy the firing criterion equation (5), but the pattern \( \mu = 3 \) does and for this pattern the post-synaptic neuron will transmit a signal further in the network. We now express the criterion for synaptic strengthening, by training the synaptic strengths according to
\[ K_{ij}(t > t_0) = K_{ij}(t) + f \ast \Theta(h_i(t_0))x_j^\mu(t_0), \quad j = 1 - 6 \] (9)
where \( \Theta(s) \) is a step function: \( = 0 \) for \( s \leq 0 \), \( = 1 \) for \( s > 1 \). \( f \) is a numerical constant (\( \approx 0.2 \)) which quantifies the measure of learning by the neuron’s synapses from the previous pattern, if this was successful. The updated synaptic strengths are now (for \( w = 0.2 \))
\[ K_{ij}(t > t_0) = [-1.2, 1.2, -0.8, 1.2, -1.2, 0.8] \] (10)
If this updated set at the \( i \) neuron is (at any \( t > t_0 \)) again presented with the earlier accepted set \( x_3^3 \), it will clearly again fire, since \( h_i(t) > 0 \). However, further than this, even when a greatly corrupted form of \( x_3^3 \) is presented, e.g.,
\[ x_1'(t > t_0) = [1, 1, 1, 1, -1, -1] \] (11)
or a very incomplete version, like
\[ x_1''(t > t_0) = [0, 0, 1, 1, -1, -1] \] (12)
in which the pre-synaptic neurons 1 and 2 do not communicate, a firing will proceed, since the output function \( h_i(t > t_0) \) will still be positive (contrary to what would have been the case before learning). This construction therefore embodies Hopfield’s idea that a learned network has a ”basin of attraction”, so that the mind can recall familiar items that are only incompletely or corruptedly presented.

The learning algorithm in equation (9) can evidently be repeatedly applied, after each successful firing, enhancing synaptic strengthening at each
subsequent stage. It may also be the case that only after a number of applications of equation (9) will a new presentation satisfy the firing criterion. (Students memorize texts by repeated reading.) It is a moot question, whether successive strengthening can also cause a deterioration of previous strengthening, but then it is an accepted fact that newer experiences can lead to an overwriting or erasure of previous memories.

Improvements in the algorithm would be taking account of forgetting: this can be done by appending an exponential decay factor to the acquired strength, as was done elsewhere [13]. Another problematic issue is that by repetition of the algorithm one apparently causes the synaptic strength grow beyond any bound; Oja ha tackled this problem by normalization of the individual synaptic strength values [14].

4 Modelling Synaptic Potentiation

In the ”Standard Model” for brain functioning after the brain receives a stimulus from an external source (which step is not our concern here) and before it activates some organ outside it (which also is not our present subject), a number of consecutive and parallel elementary steps take place. These involve the firing by a neuron, meaning the initiation of a transfer of ions or of electrical impulses, passage along an axon, arrival (of the excitation) at a synapse, this being attached to a dendrite (one of the many) belonging to a (so called, post-synaptic) neuron, which will then repeat the above process, or else arrest it depending on the magnitude of the sum of signals it registers from its dendrites. The interesting point here is that of all the items italicized above, it is the synapses that are deemed to be the clever ones, being capable of adaptation, potentiation or reduction, whereas the others are inert, unchanging, alike to manufactured items in an electronic device, such as diodes, transistors.

4.1 Brain plasticity, adaptability, or ”potentiation”

A formal treatment of the interplay between the above components of the brain was given in an influential paper by Hopfield [12] in terms of an ”energy landscape”, with origins in the physics of phase transitions. The energy landscape consists of hills and valleys in the multidimensional space of the brain system’s parameter and it varies (changes in time) with the flow of the experiences in the person.

According to Hopfield, each minimum at the valley is a local point of the system’s stability, in the sense that if some external stimuli bring the
system to the point, it will recognize that point as being identical to a
previous experience. (Example: a previously observed view will be recalled,
when the same view is presented to the the person.) The brain has "learned"
to recognize the view and adjusts itself to the old-new data.

In compliance to the physical implication of the concept of "minima
in the energy landscape", Hopfield introduced a new idea: a "basin of
attraction" exists at the close neighborhood of each minimum. This means
that to recognize a previously experienced view (or idea), its remembering,
you do not require an exact repetition of the experience, but only a close
approximation to it. In terms of the hill-valley picture, this is explained by
the dynamic behavior of the brain: the brain descends on its own to the
zenith, once it is inside a paraboloidal well.

In the following, the "basin of attraction" is calculated (approximately)
by a model based on the Hebb-Hopfield algorithm. According to this the
firing (activation) of a post-synaptic neuron depends on its potential \( x \) taking
up a value larger than a critical value \( Q \). Its actual value is determined by
the set of potentials \( x_\mu^n \) of those pre-synaptic neurons (labelled by \( n \)) that
are communicating with the post-synaptic neuron and by the values of the
synaptic strengths \( k_n \), according to a linear relation (in which the symbols
in equation (4) have been simplified as \( hN \rightarrow x \), \( K_{ij} \rightarrow k_n \), \( j \rightarrow n \) and \( i \) the
label of the post-synaptic neurons removed , since we shall be considering
a single, representative post-synaptic neuron). Thus, we have the criterion
\( x \geq Q \) for the firing of the post-synaptic neuron, with:

\[
x \equiv \sum_{n=1}^{N} k_n x_\mu^n
\]

Here \( N \) is the number of pre-synaptic neurons (of the order \( 10^{10} \)) and the
synaptic strengths \( k_n \) take (in this model, as well as in several previous ones,
e.g. [15]) values of ±1 randomly. The pre-synaptic neuron potentials \( x_\mu^n \), also
have values ±1, but (instead of regarding these as random variables) they are
arranged according to patterns as before, labelled by \( \mu \) [13]. Each pattern,
or sequence of +1’s and –1’s, presents a different experience (or trigger) to
the post-synaptic neuron (e.g., a line in a poem). (The chosen post-synaptic
neuron will in its turn transmit its firing, or the lack of it, to a subsequent
neuron, together with a number of similarly triggered other neurons, thus
becoming a pre-synaptic neuron, but this stage is not considered in the
present description of the learning process.)

The critical (or threshold) value \( Q \), for which the post-synaptic neuron
will fire will be between 0 and \( N \), which is more general than in the previous
illustrative section, in which we have used $Q = 0$. Suppose now for a moment that the presented pattern is the set of +1’s. Let us label this pattern by $\mu = 0$. Clearly, for a given chosen value of $Q$ the post-synaptic neuron will fire when at least $\frac{1}{2}(N+Q)$’s of the random synaptic strengths are +1 and at most $\frac{1}{2}(N-Q)$’s of the random synaptic strengths are −1. The probability for this to happen is (for $N + Q$ even) the binomial distribution

$$P(N, Q) = 2^{-N} C^N_{\frac{1}{2}(N+Q)} = 2^{-N} \frac{N!}{\frac{1}{2}(N + Q)! \frac{1}{2}(N - Q)!}$$  \hspace{1cm} (14)$$

and the mean width of the basin (meaning the weighted number of values for which the post-synaptic neuron will fire) is

$$W(N, Q) = \frac{1}{2} (N-Q) \sum_{\theta=0}^{\frac{1}{2}Q} (Q + 2\theta) P(N, Q + 2\theta))$$  \hspace{1cm} (15)$$

A little reflection shows that for any form of the pattern (i.e., partly +1 and partly −1) the number of firing cases and the mean basin width will be the same as calculated above.

### 4.2 After-presentation basin enhancement

To calculate the increase of the basin size due to synaptic plasticity, we write out the changed equation for the firing criterion of the post-synaptic neuron after its having been presented by the $\mu$ pattern. The consequence of the $\mu$-presentation is that the potentiated synaptic strength of the $n$’th synapse has changed from $k_n$ to $k_n + \delta k_n^\mu$ and we seek the new, extended range of the $x_n$ values (the potentials of the pre-synaptic neurons), i.e., the new “basin”, for which the criterion in equation (13) for the post-synaptic neuron will be satisfied. Writing $x^\mu$ for the potential of a post-synaptic neuron after the previous presentation of the $\mu$-pattern, we obtain the criterion

$$x^\mu = \sum_n (k_n + \delta k_n^\mu) x_n \geq Q$$  \hspace{1cm} (16)$$

We again consider (purely) for illustration purposes the case of pattern $\mu = 0$, namely that the pattern previously presented by the pre-synaptic neurons consisted of $N$ entries of +1’s, and further assume that all synapses are uniformly potentiated, in the sense that

$$\delta k_n^\mu = f k_n$$  \hspace{1cm} (17)$$
\( f \) being a positive fraction, less than one. Then the criterion in equation (16) can be written as

\[
\sum_n k_n x_n > Q - f \sum_n k_n x_n^{\mu=0}
\]

(18)

where, in the spirit of a perturbational approach, we have replaced on the right hand side the true \( x_n \) by \( x_n^{\mu=0} \). Evidently with the second term on the right subtracting, a wider range of \( x_n \) satisfies this condition than in equation (13). E.g., we can allow some of the \( x_n \) to take up negative (-1) values, even among those that previously took up positive (+1) values. Thus we see that the basin of the possible pre-synaptic neurons for the firing of the post-synaptic has become enhanced after the previous presentation, because of synaptic plasticity.

4.2.1 Graphical results

In the following figures we show for two model parameters (number of synapses attached to the post-synaptic neuron, \( N = 5, 10 \)) the original probabilities for firing of the post-synaptic neuron as function of the firing criterion (Figure 1), mean basin widths (Figure 2) before presentation of any pattern, as well as the increase in the probabilities (Figure 3) and in the mean basin width (Figure 4) after the presentation of the pattern and when a similar (but not identical) pattern is again presented.

5 Conclusion

The brain, being the hinterland to the mind’s functioning, is arguably the most enigmatic, complex and multi-component entity in our world. We have given a summary from a physicist’s angle of expectations by neurobiologists regarding the criteria (likely, minimal criteria) that are needed for the brain’s structure and functioning. We have pointed out several ambiguities in these criteria, notably in the meaning of the “economies” that are associated with the brain.

We have also constructed a model for synaptic plasticity or adaptability, based on the Hebb-Hopfield stochastic formalization of neuron firing, which shows (Figures 1-4) the enhanced range of firing (recognition) probabilities by the post-synaptic neuron after a previous presentation of a given pattern.
Figure 1: The probability, equation (14), of firing by the post-synaptic neuron as function of the firing criterion $Q$, $0 \leq Q \leq N$, where $N$ is the number of synapses (or of the pre-synaptic neurons communicating with the post-synaptic neuron). Broken lines: $N=5$, full line: $N=10$. The calculation is for probabilities before learning.

Figure 2: The mean "basin width", equation (15), for the pre-synaptic neuronal potentials plotted against firing criterion $Q$. Again: broken lines: $N=5$, full line: $N=10$. The calculation is for the widths before learning.
Figure 3: The enhanced probability, equation (18), of firing by the post-synaptic neuron as function of the firing criterion $Q$, after the presentation of the pattern. Parameter meanings as in previous figures.

Figure 4: The enhanced basin width for the pre-synaptic neurons’ potentials that satisfy the criterion ($Q$) for firing by the post-synaptic neuron after the presentation of the pattern. Parameter meanings as in previous figures.
References


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