

## General properties of the resource consumption principle of neural function

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**Summary** — It has been proposed that volumes of neural tissue may represent important processing elements. This viewpoint suggests one way that populations of synaptic elements cooperate to implement important computational capacities. I extend this view by proposing a set of computational functions for the extracellular space shared by a local population of synapses. The critical hypothesis is the existence of a hypothetical 'fluid' resource present outside synapses that must be internalized in order for a synapse to function. I outline some of the consequences of assuming that such a resource is in limited supply on short time scales.

**resource consumption / volume plasticity / synchrony / asynchrony / extracellular diffusion / cell assembly / neocortex**

### Introduction

Modern descriptions of nervous systems cast neurons, axons, dendrites, and synapses in prominent roles. These descriptions typically employ electrical circuit and computational analogies in the construction of models. Given this state of affairs, the structure and function of the mammalian brain is almost exclusively viewed through electrical and computational metaphors where the neuron plays the role of a processor that integrates information (albeit in a complex fashion), the axons act as wires, and the synapses function as complex gain control junctions. The prominent role of the neuron in all such descriptions was long ago cast as a kind of doctrine. It is not however self-evident that these are the only kinds of metaphors likely to be useful in a description of the brain function.

This paper presents an outline of a different view of neural function that focuses on the collective action of all components present in a volume of neural tissue. The physical picture explored is that of the cerebral cortex as a kind of representational media where information is stored and processed in small volumes (Montague *et al.*, 1991; Montague and Sejnowski, 1994). Pre- and post-synaptic junctions are treated as a single information bearing unit which responds (or not) to the fluctuating neurotransmitters impinging on the surrounding volume of neural tissue (fig 1). Throughout, I use the term synapse to refer to this lumped unit. The new hypotheses are: i) synapses are immersed in a fluid-like resource that they must acquire to operate and reproduce; and ii) the resource is in limited supply.

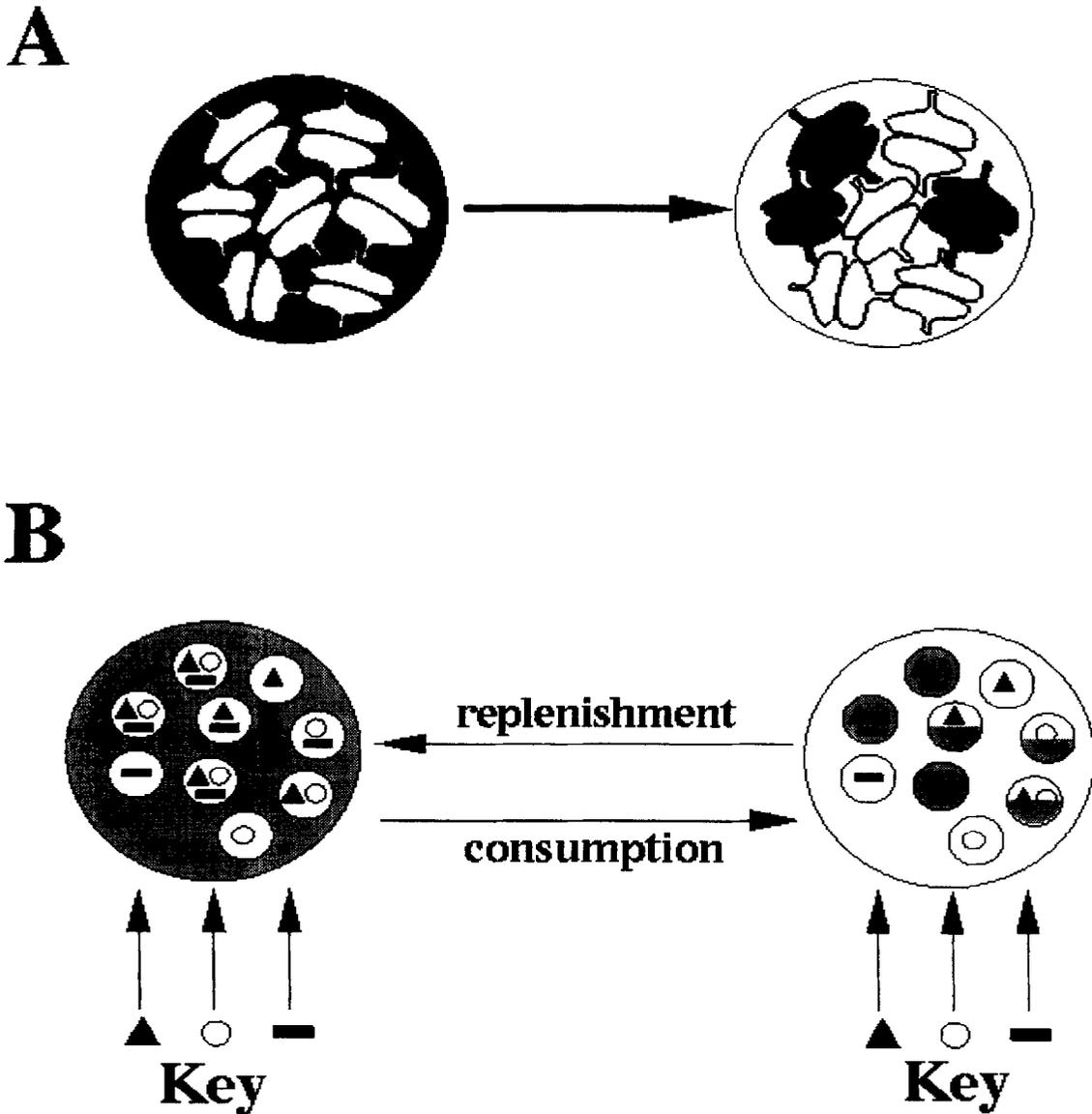
It has been suggested that extracellular calcium may act as just such a distributed fluid-like resource that is (for all practical purposes) in limited supply (Montague, 1996). Some of the consequences of these hypotheses are outlined below (also see fig 1).

### Attention-like mechanism that permits sparse representations to function

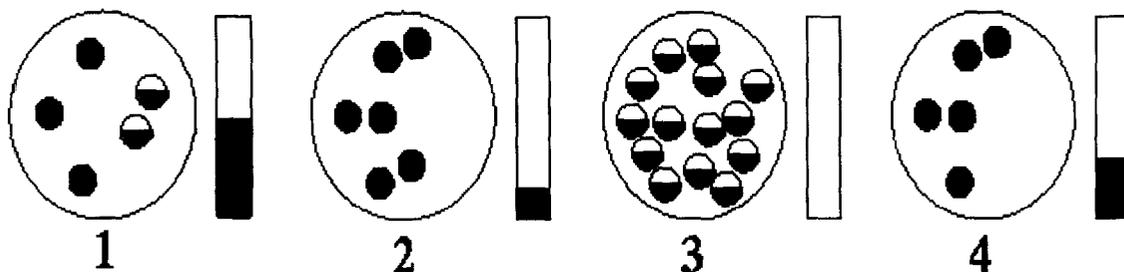
By hypothesis, the resource is in limited supply, therefore, consumption of resource by one set of synapses occurs at the expense of potential consumption by neighboring synapses in the local volume. There is only enough resource for a fraction of the synapses in any volume to operate (transmit), therefore, one consequence of hypothesis (ii) is that a competition for resource is established in local volumes of tissue. At any particular time, those synapses that have captured resource are more likely to transmit than those that have not (fig 1). In this sense, the resource acts like an attentional fluid whose distribution among synaptic and extrasynaptic compartments defines those connections to which the tissue currently attends. If most of the fluid is outside the synapses, the tissue is not attending to any of the connections in a local volume. If most of the fluid is distributed within a particular set of synapses, then the volume is attending to this set thereby diminishing its capacity to attend to another spatially overlapping set. This proposed physical property of neural tissue permits the retention of information in a small number of synapses. Depending on the availability of resource and the dynamics of its replenishment, such a mechanism would implement a strong constraint on the density of neural activity in a region of tissue.

More formally, the fluid can be cast in terms of a probability fluid that flows among compartments in a volume to define 'where' the attention of the tissue is directed. In this view, tracking the movement of the fluid identifies the response of the volume to incoming information. In this framework, the function of a tissue volume will satisfy a continuity condition:

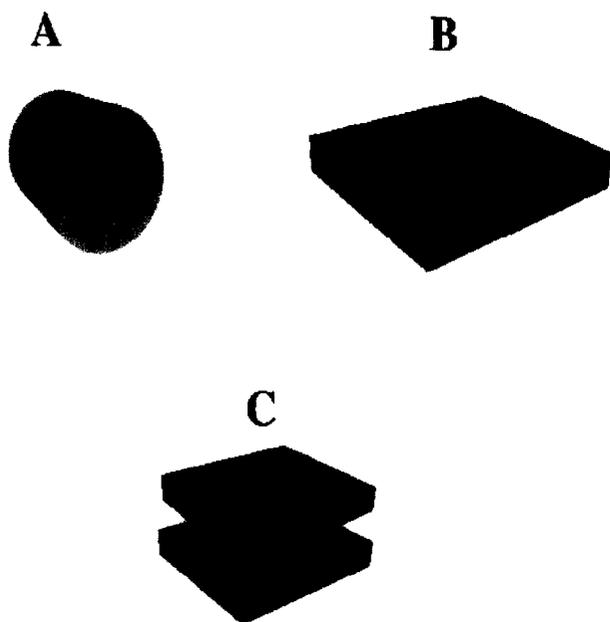
$$\dot{\rho}(\vec{x}, t) - \nabla \cdot \vec{J}(\vec{x}, t) = 0$$



**Fig 1. A.** The resource consumption principle. Synapses immersed in a homogeneously distributed resource fluid. In order to function, the resource (gray) must be moved into a synapse (white structures). Over time, (repeated) successful competition for resource leads to reproduction of the successful synapse type and removal of unsuccessful synapse types (see text). This increases the speed of resource consumption by that synapse type (resource current density into that type) and the capacity of that synapse type to control resource levels in the volume. **B.** Matching of locks and keys through a fluid-like connectivity. The collection of signals that impinge on the volume is represented as a vector  $V = (v_1, v_2, v_3, \text{etc})$  where each component of the vector  $v_i$  represents a different signal type. We call this collection of signals the key rather than an input vector since each component  $v_i$  of the key acts like a separate fluid available homogeneously throughout the volume. Different synapses are sensitive to different temporal sequences of keys because the synapses possess various combinations of receptors each sensitive to one type of fluid, *ie* one component of  $V$ . In this sense, the collection of receptors on each synapse is considered to act as a kind of code that defines the incoming information that is likely to make the synapse consume resource; this code is referred to as a combination lock. As shown, presentation of a particular key matches the combination locks of some synapses better than others causing the matching synapses to consume resource. The probability  $P_n$  that a synapse operates (transmits) is a function of the amount of resource (gray) it has captured. Independent of the physical reasons why a synapse is successful at capturing resource, the dependence on resource for function (transmission) permits the resource to act as a kind of fitness measure that can literally move among synaptic and non-synaptic compartments. At any time, the distribution of the resource acts to define those synapses to which the volume attends. The dynamics of the fluid movement could therefore be viewed as the shifting of this attention.



**Fig 2.** Long-term information storage is self-normalizing. Resource consumption by synapses in a local volume under continuous presentation of the same key. **1.** Presentation of key results in three good matches (filled circles) and two poor matches (open circles). Between 1 and 2, the good matches reproduce while the poor matches are removed. **2.** Key now causes a significant depletion of resource available to the volume and selection of functioning synapses. Because of the continuity condition (see text) the response in this fixed volume element is also quicker. **3.** Between 2 and 3, the key continues to be presented causing the over-representation of combination locks that recognize it. This effect is self-limiting (normalized) since, at some point after multiple replications, these locks consume in parallel the vast majority of the resource upon presentation of key and some fraction of them are marked for removal (see  $P_d$  in text). **4.** After removal of some fraction of the synapses that recognize the key, its presentation causes the consumption of a level of resource near the working range of the volume element.



**Fig 3.** Geometrical arrangements represent implicit computations or relationships. Separate resource consumption volumes easily take advantage of various geometrical arrangements. **A.** In this example, volume 1 (dark central cylinder) was trained separately on examples from category 1 and volume 2 (gray cylindrical annulus) was trained separately on category 2. Volume 2 was trained with twice as much resource as volume 1. Once volumes 1 and 2 were deformed and made into juxtaposed cylinder and surrounding annulus, changes in synapse number were not permitted and the resource level available to the entire assembly was set to the level on which volume 2 (annulus) was trained. **B.** After training, the juxtaposed modules were put into a slab and the response of the assembly was tested under a variety of conditions. Presentation of examples from category 1 alone consumes all the resource available to both volumes. Presentation of examples from category 1 alone activated synapses in the central cylinder, however, this did not consume all the resource. Presenting category 1 examples followed by category 2 activated category 1 synapses and then a subset of category 2 synapses. Reversing the order ( $2 \rightarrow 1$ ) activated category 2 synapses but not 1 since activation of 2 completely depleted the resource in the interior cylindrical region. This example shows that separately trained modules can take advantage of the relationships that exist through the shared resource without the cost of extra connections. **C.** The example in **A** and **B** can be extended to larger scale mapped areas. Multiple resource consumption engines can be trained and arranged in a mapped array. By juxtaposing two such arrays, they are forced to share the same resource. This capacity allows for the easy representation of hierarchical or otherwise structured category relationships.

where  $\dot{\rho}(\vec{x}, t)$  is the rate of change of resource density and  $\mathcal{J}(\vec{x}, t)$  is the resource flux. This continuity condition asserts that resource is not created or destroyed, however, alone, the continuity condition is not particularly interesting. It is more useful to characterize the dynamics of how the resource partitions into different identifiable compartments (eg synapses, glial cells, etc) and how this redistribution depends on some characterization of the information the impinges on a volume. These possibilities are under active investigation (Montague and Dayan, unpublished observations).

### Normalization and sparse representations are a requirement of the hypotheses

As proposed (Montague, 1996), long-term memory is maintained in the abundance of a synapse type, therefore, changes in the abundance of a particular type of synapse constitute learning. Synapses that consume resource in the same fashion through time would constitute a type. The idea that the abundance of a synapse type holds all the information is somewhat misleading since abundance is only a pertinent property when the synapses are sufficiently close in the tissue to permit them to share resource. This consideration highlights the important role played by geometrical arrangement of synapses in a tissue volume.

The resource acts as a kind of final assay of the fitness of a synapse type, hence, the probability that a synapse operates (transmits)  $P_o$ , reproduces (makes a copy)  $P_r$ , or retracts (dies)  $P_d$ , will all be functions of the amount of resource possessed by the synapse (Montague, 1996). Accordingly, we let:

$$P_o(E_i(t), \beta(t)) = \frac{1}{1 + \exp(\beta(t) E_i(t) + b)}$$

where  $P_o$  is the probability that synapse  $i$  operates (transmits) at time  $t$ ,  $E_i$  is the amount of resource possessed by synapse  $i$ . We take the probability that synapse  $i$  does not operate (transmit) at time  $t$  as  $1 - P_o$ .  $P_d = P_r$  are taken as fixed probabilities per unit time. Under this model, the fixed amount of resource institutes a normalization condition on two different time scales: 1) shorter time scales: synapses transmit (or not) as a function of the amount of resource they have captured, however, there is not enough resource for all synapses in a volume to operate so that

the maximum number of active synapses at any time is limited; 2) longer time scales: as the abundance of a synapse type is increased, the amount of available resource imposes a maximum limit on the total number. In the case where synapse numbers were actually changed exponentially (sprouting), a volume of tissue could quickly learn from a small amount of input data.

### Conclusion

The new proposal presented here does not discard the neuron as one pertinent structural unit in nervous system function, however, it suggests that all elements in a tissue volume act together. The way the proposal works is through the assumption of a kind of final common path for deciding which connections are working at any given time — a fluid-like shared resource that must be acquired. Three important properties of the theory were outlined above: 1) the resource normalizes synaptic activity on short time scales (fig 1); 2) maintains long-term information in a small number of synapses (fig 2) (sparse representations); and 3) provides a mechanism through which such sparse representations can actually function. Although the focus has been on the behavior of the model in an isolated volume of tissue, the idea of a shared, fluid resource implements interactions that extend directly through the tissue. Figure 3 shows the results of preliminary computational experiments in which the geometrical relationships among tissue volumes can be used to account for some aspects of hierarchical and modular structure that exist in the cortex. The possibilities for the resource consumption principle are just now being explored - the capacity of this new metaphor to extend descriptions of brain function remains to be seen.

### References

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