

Three-dimensional synaptic distributions influence neural processing through the resource consumption principle

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Introduction

Our recent work on the mammalian cerebral cortex has focused on signals that define processing that takes place throughout a volume of neural tissue (Montague *et al.*, 1991; Montague and Sejnowski, 1994; Montague *et al.*, 1994; Montague, 1996a). As discussed in the companion paper (Montague, 1996b), this view of neural function extends standard neuron-centered views and it possesses some features of other approaches that appeal to selectional schemes (*eg* Changeux and Danchin, 1973). Under the resource consumption principle, single synapses act as units with pre-existing sensitivities to fluctuating neurotransmitter delivery and synapses must acquire a shared fluid-like resource in order to operate (transmit), reproduce (sprout), or die (retract) (Montague, 1996). Synapses cooperate and compete directly through tissue space by means of the shared resource. One working hypothesis of the theory is that each synapse's collection of receptors defines the sequence and duration of incoming neurotransmitters that is likely to make the synapse consume resource and hence operate. In this sense, the collection of receptors possessed by a synapse acts as a label or code for a particular synapse type. As previously suggested, extracellular calcium displays features that make it a possible candidate for a shared, but limited, extracellular resource (Montague, 1996a). The main idea is a simple one in which many different physical features define a synapse's capacity to obtain resource: the arrival of a spike along a parent axon followed by opening of voltage sensitive channels, binding of neurotransmitter, influence of intracellular signaling cascades, participation in local anatomical motifs, etc. The resource consumption principle avoids making explicit reference to these possible reasons that a synapse has consumed resource and simply lets the total resource captured define which synapses are likely to be working. In this sense, the theory is a strongly selective one: there is no specification for which synapses will

work or not in a particular volume of tissue. The resource acts as a kind of fitness assay for synapses: whether or not one can identify the exact reason that a synapse was fit in a particular context is not relevant to this description.

Simulation methods

In this paper we present some preliminary examples of the effects of three-dimensional spatial distribution of synapses on the ability of a synaptic code to compete for resource in a region of tissue. We have performed computer simulations of synapses and resource 'molecules' in a cubical volume of neural tissue. In these simulations, the volume is divided into voxels with an equal number of voxels along each dimension. Each voxel contains intracellular and extracellular compartments. On each iteration, resource molecules diffuse between voxels, move into synapses matching the signals impinging on the volume, or reflect from the walls of the simulated volume. The choice of voxel size and diffusion constant sets the time scale of each iteration.

Results

To demonstrate the effects of geometry on consumption, we simulate 1250 perfectly matching synapses throughout the volume, *ie* the signal impinging on the volume matches perfectly the codes of these synapses. The other synapses in the volume do not match the therefore do not participate in consumption. For the 1250 matching synapses, figure 1 shows how changing the volume of the region through which they are distributed changes the time course of resource consumption from the volume, an effect which can be anticipated analytically. If the survival of a particular synaptic code relied on consumption at another code's expense, it can be seen that a more sparse representation in a volume is advantageous.

Figure 2 shows the effects of shape for four different synaptic distributions within volumes: random (as in

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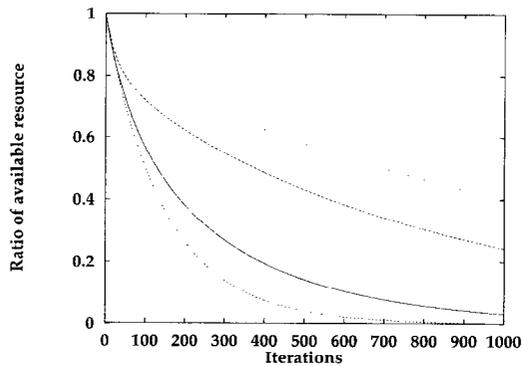


Fig 1. Influence of synaptic density. Bottom trace, 1250 synapses that matched key ϕ (input vector; see companion paper (Montague, 1996b) for description of key) were randomly distributed within a cube of $50 \times 50 \times 50$ voxels. The key ϕ was presented at each time step and each of the 1250 matching synapses consumed all the extracellular resource within their voxel. This model for consumption is analogous to a kind of transport mode which might require energy; resource is acquired by a synapse according to the degree of match between the synapse code and the key without dependence on the amount currently possessed by the synapse or the history of resource consumption by the synapse. Diffusion of the extracellular resource partially replenished empty voxels in between presentations of ϕ . Plotted is the fraction of extracellular resource in the large volume, V . Upper traces, the random distribution of the same 1250 synapses within successively smaller cubes of side length 40, 30, and 25 voxels within the $50 \times 50 \times 50$ volume, respectively. For this example, no noise or replenishment was represented.

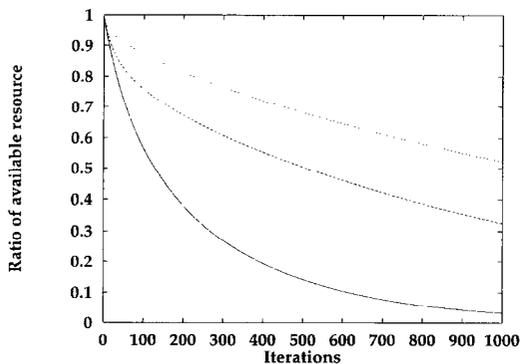
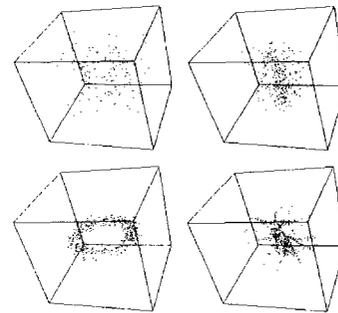


Fig 2. Effect of synaptic distribution shape on consumption. Bottom trace, resource depletion in the entire volume due to the random distribution of 1250 synapses in a $40 \times 40 \times 40$ voxel cube. This cube exists within a larger volume of $50 \times 50 \times 50$ to minimize the influence of border effects. Middle trace, the 1250 synapses matching the presented key are now distributed in a cylindrical volume. Upper trace, extracellular resource depletion when the 1250 synapses are distributed in an annular volume (see fig 3A for illustration).

fig 1), cylindrical, annular, and a spatial distribution defined by the dendritic arbor of a real stellate cell from cat cortex. The sparser distributions deplete resource from the volume in a smaller number of iterations suggesting that certain axonal and dendritic geometries play different functional roles under the constraints imposed by the resource consumption principle.

Lastly, we illustrate how resource consumption may translate into synapse operation, *ie* transmission. The probability that a synapse will transmit is taken to be a function of the amount of resource it possesses, in this case, the dependence is sigmoidal (see companion paper, Montague, 1996b). As can be seen in figure 3, different geometries yield different time courses in which synapses begin to operate. These effects result from the continuity condition described in the com-

A



B

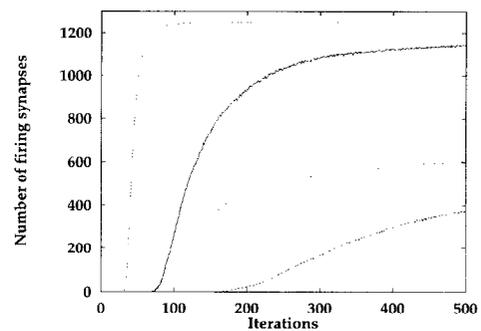


Fig 3. Effect of synaptic distribution shape on transmission. **A.** Different geometrical distributions. Random (upper left), cylindrical (upper right), toroidal (lower left), and mapped onto dendrites of stellate cell (lower right). **B.** Effect on transmission times and delays.

A sigmoidal function: $P_o = \frac{1}{1 + e^{-2C+100}}$ determined each synapse's

probability of operation (transmission) as a function of intracellular resource C . The traces, in order from bottom to top, represent a toroidal, cylindrical, cellular, and random distribution of 700 synapses in a cube (40 voxels per side within a 50 voxels per side volume). Tightly packed synapses inhibited each other's consumption, with the result that the synapses which became operational first were those with more sparse distributions.

panion paper (Montague, 1996b) tightly packed synapses possessing the same code steal resource from one other, mutually hampering chances for transmission.

Conclusion

We have presented some simple illustrative examples of the kinds of effects expected from the theoretical framework presented in the companion paper (Montague, 1996b), both of which address some implications of the resource consumption principle. Future work will give richer illustrations of the way information may be represented in three-dimensional tissue space under a set of constraints such as those described in the resource consumption principle.

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