

Statistical mechanics of neocortical interactions: Constraints on 40-Hz models of short-term memory

Lester Ingber*

Lester Ingber Research, P.O. Box 857, McLean, Virginia 22101

(Received 20 March 1995; revised manuscript received 30 May 1995)

Calculations presented in L. Ingber and P.L. Nunez, *Phys. Rev. E* **51**, 5074 (1995) detailed the evolution of short-term memory in the neocortex, supporting the empirical 7 ± 2 rule of constraints on the capacity of neocortical processing. These results are given further support when other recent models of 40-Hz subcycles of low-frequency oscillations are considered.

PACS number(s): 87.10.+e, 05.40.+j, 02.50.-r, 02.70.-c

I. BACKGROUND

In a recent paper [1], high-resolution path-integral calculations of a previously developed model of short-term memory (STM) in the neocortex were presented. These calculations, made possible with supercomputer resources, supplanted similar calculations [2] and supported coarser estimates made a decade earlier [3,4]. A more detailed description of the theoretical basis for these calculations and a description of other phenomena, e.g., electroencephalographic (EEG) data, can be found in previous papers in this series of statistical mechanics of neocortical interactions (SMNI) [2,5–16]. The SMNI approach is to develop mesoscopic scales of neuronal interactions at columnar levels of hundreds of neurons from the statistical mechanics of relatively microscopic interactions at neuronal and synaptic scales, poised to study relatively macroscopic dynamics at regional scales as measured by scalp EEG. In SMNI, the derived firings of columnar activity, considered as order parameters of the mesoscopic system, develop multiple attractors, which illuminate attractors that may be present in the macroscopic regional dynamics of the neocortex.

The SMNI calculations are of minicolumnar interactions among hundreds of neurons, within a macrocolumnar extent of hundreds of thousands of neurons. Such interactions take place on time scales of several τ , where τ is on the order of 10 msec (of the order of time constants of cortical pyramidal cells). This also is the observed time scale of the dynamics of STM. We hypothesized that columnar interactions within and/or between regions containing many millions of neurons are responsible for phenomena at time scales of several seconds. The nonlinear evolution was calculated at relatively finer temporal scales, giving a base of support for the phenomena observed at the coarser temporal scales, e.g., by establishing mesoscopic attractors at many macrocolumnar spatial locations to process patterns at larger region domains.

As pointed out in a recent paper, long-ranged minicolumnar circuitry across regions and across macro-

columns within regions is quite important in the neocortex and those SMNI calculations only represented a model of minicolumnar interactions within a macrocolumn [1]. Therefore, only the first few τ foldings should be considered as having much physical significance. It must be assumed that other effects, e.g., those contained in long-ranged neocortical circuitry, should suffice to “replenish” these memories, to account for the observed durations of many tenths of a second to many seconds of STM.

A recent proposal has been advanced that STM is processed by information coded in approximately 40-Hz (approximately 2.5 foldings of τ) bursts per stored memory, permitting up to seven such memories to be processed serially within single waves of lower frequencies on the order of 5 to 12 Hz [17]. To account for the observed duration of STM, those authors propose that observed after-depolarization (ADP) at synaptic sites, affected by the action of relatively long-time acting neuromodulators, e.g., acetylcholine and serotonin, acts to regularly “refresh” the stored memories in subsequent oscillatory cycles. A recent study of the action of neuromodulators in neocortex supports the premise of their effects on broad spatial and temporal scales [18], but the ADP model is much more specific in its proposed spatial and temporal influences.

Section II gives a set of comparisons between the SMNI and ADP approaches, organized according to several experimental issues. Section III presents the short but important conclusion that a confluence of models gives us a deeper understanding of STM, SMNI presenting statistical constraints on large-scale neuronal interactions, while other finer-resolution approaches present plausible models for specific neuronal interactions.

II. SMNI AND ADP APPROACHES

A. 7 ± 2 rule

STM is observed to transpire on the order of tenths of a second to seconds, generally limited to the retention of 7 ± 2 items [19]. This is true even for apparently exceptional memory performers who, while they may be capable of more efficient encoding and retrieval of STM, and

*Electronic address: ingber@alumni.caltech.edu

while they may be more efficient in “chunking” larger patterns of information into single items, nevertheless are limited to a STM capacity of 7 ± 2 items [20]. Mechanisms for various STM phenomena have been proposed across many spatial scales [21].

SMNI addresses the 7 ± 2 rule as the number of attractors possible in minicolumnar interactions, using synaptic and neuronal parameters taken from experimental data. These attractors are most-likely states of an evolving conditional probability distribution of columnar firings.

The ADP model is based on neural network simulations. The model is based on the memory storage possible within single neurons, using changes in phases of cell firings to store information across the network. Both assumptions must of course be considered as tentative, awaiting more conclusive experimental confirmation than that offered in the present formulation of the ADP model. Furthermore, it is well known from many neural network studies that ensembles of neurons can simultaneously support multiple memories [22], so that it is unlikely that just serially connecting 40-Hz subcycles within larger oscillatory cycles can provide the 7 ± 2 constraint.

The SMNI approach gives a consistent interpretation of STM across the many observed levels of information processes that presumably take place across most of the neocortex. For example, this is the reasonable interpretation of how the above phenomenon of “chunking” is made possible at various levels of abstraction. The ADP approach must require similar neuromodulator controls over all regions of the neocortex, which does not seem likely [18].

The SMNI approach by itself fails to account for the duration of STM. Early papers [3,4], suggested the possibility of sustenance of STM over epochs of tens of seconds just due to localized columnar interactions, but it was already clear that longer-ranged influences were important to the development of the SMNI approach [5–7].

More recent calculations show that this duration of STM may not be possible if only localized columnar interactions are considered [1,2]. After approximately 5τ , the clear separation between peaks of most-likely states in the evolving conditional probability distribution soon overlap. After approximately 10τ , the separation hardly exists. All four models considered, representing dominant inhibition, dominant excitation, a “balanced” case in between these two (model BC' illustrated here), and the latter for the visual neocortex, exhibit similar decays of their peaks over these time scales. Future calculations, including all nonlinear SMNI effects might change this numerical result, but still the action of long-ranged neuron-neuron and diffuse neuromodulator interactions are known to be important to neocortical function, and they must be addressed.

The ADP model has an explicit mechanism for sustenance of firings into durations of tens of seconds. Unfortunately, since some neuromodulators can act for much longer times, the ADP model can only put an upper bound on STM duration by limiting the model to specific neuromodulators, which may not affect all neocortex involved with STM.

The ADP approach states that observed STM dura-

tions are the result of how 40 Hz signals can be stacked within waves of α to θ oscillations (5 to 12 Hz). This appears to be a quite naive view of α generation in the neocortex, as it is extremely likely that there are many generators of α across many scales of interaction [23], e.g., ranging from hemispheric global resonance effects [24] to local columnar generators [6,7], and to more specific neuronal interactions [25].

B. 4 ± 2 rule

The authors of the ADP model, in their Ref. 25, acknowledge another neuroscientist for making them aware of the pioneering work on memory limits [19]. However, their paper does not mention other pioneering work of the 4 ± 2 rule [26]. The 7 ± 2 rule is verified for acoustical STM, but for visual or semantic STM, which typically require longer times for rehearsal in an hypothesized articulatory loop of individual items, STM capacity appears to be limited to 4 ± 2 . The 4 ± 2 rule is not mentioned in the ADP model.

In SMNI, the 4 ± 2 rule is established by virtue of detailed calculations using the experimental observation that the number of neurons per minicolumn in the visual cortex is about twice that in other regions of the neocortex [1–4]. While each attractor of the conditional probability distribution becomes sharper and more stable, the number of effective attractors is reduced to within the 4 ± 2 constraint.

C. Primacy versus recency rule

Another interesting phenomenon of STM capacity explained by the SMNI is the primacy versus recency effect in STM serial processing, wherein first-learned items are recalled most error-free, with last-learned items still more error-free than those in the middle [27].

In the SMNI approach, the basic assumption is made that a pattern of neuronal firing that persists for many τ cycles is a candidate to store the “memory” of activity that gave rise to this pattern. If several firing patterns can simultaneously exist, then there is the capability of storing several memories. The short-time conditional probability distribution derived for the neocortex is the primary tool to seek such firing patterns. The deepest minima of the Lagrangian are more likely accessed than the others of this probability distribution, and these valleys are sharper than the others; i.e., they are more readily accessed and sustain their patterns against fluctuations more accurately than the relatively more shallow minima. The more recent memories or newer patterns may be presumed to be those having synaptic parameters more recently tuned and/or more actively rehearsed.

It is difficult to see how invoking the ADP mechanism can explain the primacy versus frequency rule, since the ADP mechanism assumes that newly acquired memories simply replace old ones, and it also assumes that memories are scanned serially [17].

The primacy versus recency rule is verified for acoustical STM, but visual or semantic STM typically requires longer times for rehearsal in an hypothesized articulatory

loop of individual items [26]. Experimental paradigms that do not account for the 4 ± 2 rule of visual STM of course will tend to lose the recency part of this rule.

D. Large scale influences of STM

The SMNI model develops STM as attractors of the conditional probability of firings, and these attractors are candidates for influencing large scale circuitry across regions of the neocortex [1]. This concept was tested by demonstrating that these attractors could fit EEG data taken under conditions of stressing STM in subjects [13]. The statistical results of that study negated suggestions in the previous literature that the EEG by itself might determine a genetic predisposition to alcoholism. More recent studies on this clinical problem look for multiple factors beyond just EEG, although EEG may still be an extremely important diagnostic component of such studies.

The ADP model has not yet been tested with any clinical source of data.

III. CONFLUENCE OF MODELS

SMNI details the capability of minicolumnar activity to develop multiple memories of capacity 7 ± 2 with duration on the order of tenths of a second. These memories are described as most-likely states of an evolving probability distribution of minicolumnar firings. It also details an explanation of related phenomena, e.g., the observed random access phenomena of these memories, the 4 ± 2 rule, the primacy versus recency rule, and the influence of STM in observed EEG patterns. The SMNI does not detail any specific synaptic or neuronal mechanisms that

might refresh these most-likely states to reinforce multiple short-term memories. However, the calculated evolution of states is consistent with the observation that an oscillatory subcycle of 40 Hz may be the bare minimal threshold of self-sustaining minicolumnar firings before they begin to degrade.

The mechanism of ADP details a specific synaptic mechanism that, when coupled with additional proposals of neuronal oscillatory cycles of 5–12 Hz and oscillatory subcycles of 40 Hz, can sustain these memories for longer durations on the order of seconds. By itself, ADP does not provide a constraint such as the 7 ± 2 rule. The ADP approach does not address the observed random access phenomena of these memories, the 4 ± 2 rule, the primacy versus recency rule, or the influence of STM in observed EEG patterns.

The SMNI and ADP models are complementary to the understanding of STM. Research is in progress to implement various synaptic mechanics into the SMNI framework. For example, the SMNI approach has been proposed to study minicolumnar interactions across macrocolumns and across regions. This could be approached with a mesoscopic neural network using a confluence of techniques drawn from the SMNI, modern methods of functional stochastic calculus defining nonlinear Lagrangians, adaptive simulated annealing (ASA) [28], and parallel-processing computation, to develop a generic nonlinear stochastic mesoscopic neural network (MNN) [14]. The MNN can be used to overlap the spatial scales studied by the SMNI with the finer spatial scales typically studied by other relatively more microscopic neural networks. At this scale, such models as ADP are candidates for providing an extended duration of firing patterns within the microscopic networks.

-
- [1] L. Ingber and P.L. Nunez, *Phys. Rev. E* **51**, 5074 (1995).
 [2] L. Ingber, *Phys. Rev. E* **49**, 4652 (1994).
 [3] L. Ingber, *Phys. Rev. A* **29**, 3346 (1984).
 [4] L. Ingber, *Phys. Rev. A* **31**, 1183 (1985).
 [5] L. Ingber, *J. Social Biol. Struct.* **4**, 211 (1981).
 [6] L. Ingber, *Physica D* **5**, 83 (1982).
 [7] L. Ingber, *Phys. Rev. A* **28**, 395 (1983).
 [8] L. Ingber, *IEEE Trans. Biomed. Eng.* **32**, 91 (1985).
 [9] L. Ingber, *Innov. Tech. Biol. Med.* **6**, 753 (1985).
 [10] L. Ingber, in *Computer Simulation in Brain Science: Proceedings, University of Copenhagen, 1986*, edited by R. Cotterill (Cambridge University Press, London, 1988), pp. 513–533.
 [11] L. Ingber, in *Systems with Learning and Memory Abilities: Proceedings, University of Paris, 1987*, edited by J. Delacour and J.C.S. Levy (Elsevier, Amsterdam, 1988), p. 387.
 [12] L. Ingber and P.L. Nunez, *Math. Comput. Model.* **13**, 83 (1990).
 [13] L. Ingber, *Phys. Rev. A* **44**, 4017 (1991).
 [14] L. Ingber, *Phys. Rev. A* **45**, R2183 (1992).
 [15] L. Ingber, in *Neocortical Dynamics and Human EEG Rhythms*, edited by P.L. Nunez (Oxford University Press, New York, 1995), p. 628.
 [16] L. Ingber, *Electroencephal. Clin. Neurophysiol.* (to be published).
 [17] J.E. Lisman and M.A.P. Idiart, *Science* **267**, 1512 (1995).
 [18] R.N. Silberstein, in *Neocortical Dynamics and Human EEG Rhythms*, edited by P.L. Nunez (Oxford University Press, New York, 1995), p. 628.
 [19] G.A. Miller, *Psychol. Rev.* **63**, 81 (1956).
 [20] K.A. Ericsson and W.G. Chase, *Am. Sci.* **70**, 607 (1982).
 [21] H. Eichenbaum, *Science* **261**, 993 (1993).
 [22] J. Hertz, A. Krogh, and R.G. Palmer, *Introduction to the Theory of Neural Computation* (Addison-Wesley, Redwood City, 1991).
 [23] P.L. Nunez, *Neocortical Dynamics and Human EEG Rhythms* (Oxford University Press, New York, 1995).
 [24] P.L. Nunez, *Electric Fields of the Brain: The Neurophysics of EEG* (Oxford University Press, London, 1981).
 [25] A. Van Rotterdam, F.H. Lopes da Silva, J. van der Ende, M.A. Viergever, and A.J. Hermans, *Bull. Math. Biol.* **44**, 283 (1982).
 [26] G. Zhang and H.A. Simon, *Memory & Cognition* **13**, 193 (1985).
 [27] B.B. Murdock, Jr., *Psychol. Rev.* **90**, 316 (1983).
 [28] L. Ingber, Lester Ingber Research report [ftp.alumni.caltech.edu: /pub/ingber/ASA-shar, ASA-shar.Z, ASA.tar.Z, ASA.tar.gz, ASA.zip], 1993.