

Mini-Symposium

From Invertebrate Olfaction to Human Cognition: Emerging Computational Functions of Synchronized Oscillatory Activity

Ole Paulsen^{1,2} and Terrence J. Sejnowski^{3,4}

¹Department of Physiology, Anatomy, and Genetics, University of Oxford, Oxford OX1 3PT, United Kingdom, ²Centre for the Biology of Memory, Norwegian University of Science and Technology, NO-7489 Trondheim, Norway, ³Howard Hughes Medical Institute, Salk Institute for Biological Studies, La Jolla, California 92037, and ⁴Department of Biology, University of California, San Diego, La Jolla, California 92093

Key words: cognition; memory; olfaction; network; oscillation; synchronization

Oscillations and synchronization are fundamental processes in many biological systems, from prokaryotes to humans on time-scales that range from milliseconds to days (Winfrey, 2001; Gillette and Sejnowski, 2005). In nervous systems, synchronized oscillations are prevalent in active assemblies of neurons. They have been recorded in a wide variety of species, from invertebrates to humans. Although the function of some of these oscillations appears obvious, such as those related to breathing and locomotion, the functions of others, such as those related to human cognition, remain elusive. The human cortex generates oscillations in many frequency ranges, as evidenced by electroencephalography (EEG). Much progress has been made since the original description of the human EEG (Berger, 1929), and we are beginning to understand the mechanisms underlying network oscillations in the mammalian cortex. Recent experiments have shifted focus from studying pacemaker mechanisms to studying the interaction of multiple local oscillators and have revealed an important role of GABAergic interneurons in such local network oscillations. These and other recent developments have been extensively reviewed previously (Steriade et al., 1993; Steriade, 2000; Buzsaki, 2002; Whittington and Traub, 2004; Mann and Paulsen, 2005; Somogyi and Klausberger, 2005). However, we are still far from understanding the function of these oscillations. The computational richness and evolutionary conservation of network oscillations suggest that they are used in neural information processing. This series of three mini-symposia aims to discuss possible functions of network oscillations in relation to their computational roles.

Network oscillations in olfactory systems involving local inhibitory interneurons have proven useful in the study of their computational roles. First, sensory-induced oscillatory activity was discovered in the olfactory bulb >60 years ago (Adrian, 1942), and the underlying mechanisms have been investigated in

considerable detail. Second, oscillatory activity in olfaction arises early in phylogeny and appears to be evolutionarily conserved, suggesting they are functionally important. Studies in invertebrates have been particularly important in revealing the types of computations that could be performed during oscillatory activity, as discussed in the first mini-symposium by Gelperin (2006).

Whereas evidence is accumulating for the importance of oscillations in olfactory systems of various species, it is unresolved whether they have any function in the human cerebral cortex. However, oscillations are a prominent feature of mammalian cortical activity. Two rhythms that show particularly strong behavioral correlates are the theta (4–8 Hz) and gamma (30–100 Hz) rhythms, both of which have been linked to cognitive functions. The gamma rhythm has recently been linked specifically to the blood oxygen level-dependent functional magnetic resonance imaging (fMRI) signal (Logothetis et al., 2001; Foucher et al., 2003), enabling links to be made between fMRI studies and the local network activity that occurs during cognitive processing. Intracranial EEG recordings, taken from neurosurgical patients, have provided strong evidence for locally generated brain oscillations in both hippocampus and neocortex. Along with scalp EEG recordings, these studies show synchronous oscillations in the theta and gamma frequency bands that are modulated by behavioral and task variables, as discussed by Kahana in the second mini-symposium (Kahana, 2006).

Based on converging evidence from different species, one can begin to consider the computational advantages of oscillatory synchronization and to seek general principles. Network oscillations may take part in representing information, regulate the flow of information in neural circuits, and help store and retrieve information in synapses distributed throughout cortical networks. These three ideas are discussed in the third mini-symposium by Sejnowski and Paulsen (2006).

References

- Adrian ED (1942) Olfactory reactions in the brain of the hedgehog. *J Physiol (Lond)* 100:459–473.
- Berger (1929) Über das Elektrenkephalogramm des Menschen. *Arch Psychiat Nervenkr* 87:527–570.
- Buzsaki G (2002) Theta oscillations in the hippocampus. *Neuron* 33:325–340.
- Foucher JR, Otzenberger H, Gounot D (2003) The BOLD response and the

Received Sept. 3, 2005; revised Dec. 2, 2005; accepted Dec. 17, 2005.

This mini-symposium series is based on a symposium entitled *Network Oscillations: Of Mollusks, Mice, and Men*, presented at the Society for Neuroscience Annual Meeting, Washington, DC, November 12–16, 2005. We apologize to all colleagues whose work we could not cite because of space constraints.

Correspondence should be addressed to Dr. Ole Paulsen, University of Oxford, Department of Physiology, Anatomy, and Genetics, Sherrington Building, Parks Road, Oxford OX1 3PT, UK. E-mail: ole.paulsen@physiol.ox.ac.uk.

DOI:10.1523/JNEUROSCI.3737-05a.2006

Copyright © 2006 Society for Neuroscience 0270-6474/06/261661-02\$15.00/0

- gamma oscillations respond differently than evoked potentials: an interleaved EEG-fMRI study. *BMC Neurosci* 4:22.
- Gelperin A (2006) Olfactory computations and network oscillations. *J Neurosci* 26:1663–1668.
- Gillette MU, Sejnowski TJ (2005) Biological clocks coordinately keep life on time. *Science* 309:1196–1198.
- Kahana MJ (2005) The cognitive correlates of human brain oscillations. *J Neurosci* 26:1669–1672.
- Logothetis NK, Pauls J, Augath M, Trinath T, Oeltermann A (2001) Neurophysiological investigation of the basis of the fMRI signal. *Nature* 412:150–157.
- Mann EO, Paulsen O (2005) Mechanisms underlying gamma (“40 Hz”) network oscillations in the hippocampus: a mini-review. *Prog Biophys Mol Biol* 87:67–76.
- Sejnowski TJ, Paulsen O (2006) Network oscillations: emerging computational principles. *J Neurosci* 26:1673–1676.
- Somogyi P, Klausberger T (2005) Defined types of cortical interneurone structure space and spike timing in the hippocampus. *J Physiol (Lond)* 562:9–26.
- Steriade M (2000) Corticothalamic resonance, states of vigilance and mentation. *Neuroscience* 101:243–276.
- Steriade M, McCormick DA, Sejnowski TJ (1993) Thalamocortical oscillations in the sleeping and aroused brain. *Science* 262:679–685.
- Whittington MA, Traub RD (2003) Interneuron diversity series: inhibitory interneurons and network oscillations in vitro. *Trends Neurosci* 26:676–682.
- Winfree AT (2001) *The geometry of biological time*, Ed 2. New York: Springer.