Available at www.sciencedirect.com
SciVerse ScienceDirect
journal homepage: www.elsevier.com/locate/modo
ELSEVIER
MECHANISMS OF DEVELOPMENT

Review

Development of coherent neuronal activity patterns in mammalian cortical networks: Common principles and local hetereogeneity

Alexei V. Egorov *, *Andreas Draguhn*

Institute of Physiology and Pathophysiology, University of Heidelberg and Bernstein Center for Computational Neuroscience (BCCN) Heidelberg/Mannheim, D-69120 Heidelberg, Germany

A R T I C L E I N F O

Article history:
Available online 29 September 2012

Keywords:
Postnatal development
Network oscillations
Intrinsic bursts
Hippocampus
Entorhinal cortex

A B S T R A C T

Many mammals are born in a very immature state and develop their rich repertoire of behavioral and cognitive functions postnatally. This development goes in parallel with changes in the anatomical and functional organization of cortical structures which are involved in most complex activities. The emerging spatiotemporal activity patterns in multi-neuronal cortical networks may indeed form a direct neuronal correlate of systemic functions like perception, sensorimotor integration, decision making or memory formation. During recent years, several studies – mostly in rodents – have shed light on the ontogenesis of such highly organized patterns of network activity. While each local network has its own peculiar properties, some general rules can be derived. We therefore review and compare data from the developing hippocampus, neocortex and – as an intermediate region – entorhinal cortex. All cortices seem to follow a characteristic sequence starting with uncorrelated activity in uncoupled single neurons where transient activity seems to have mostly trophic effects. In rodents, before and shortly after birth, cortical networks develop weakly coordinated multineuronal discharges which have been termed synchronous plateau assemblies (SPAs). While these patterns rely mostly on electrical coupling by gap junctions, the subsequent increase in number and maturation of chemical synapses leads to the generation of large-scale coherent discharges. These patterns have been termed giant depolarizing potentials (GDPs) for predominantly GABA-induced events or early network oscillations (ENOs) for mostly glutamatergic bursts, respectively. During the third to fourth postnatal week, cortical areas reach their final activity patterns with distinct network oscillations and highly specific neuronal discharge sequences which support adult behavior. While some of the mechanisms underlying maturation of network activity have been elucidated much work remains to be done in order to fully understand the rules governing transition from immature to mature patterns of network activity.

* Corresponding author. Address: Institute of Physiology and Pathophysiology, University of Heidelberg, Im Neuenheimer Feld 326, D-69120 Heidelberg, Germany. Tel.: +49 6221 544053; fax: +49 6221 546364.
E-mail address: alexei.egorov@urz.uni-heidelberg.de (A.V. Egorov).
0925-4773/$ - see front matter
http://dx.doi.org/10.1016/j.mod.2012.09.006

Contents

1. Introduction

Coherent multi-neuronal activity patterns are a hallmark of neuronal networks. Evidence from mature, behaving animals suggests that all behavioral and cognitive functions are accompanied by highly ordered and task-specific spatiotemporal activity in local or distributed circuits of the brain. Recent progress in electrical, genetic and optogenetic interference techniques has provided first direct insights into the causal relationship between network-level activity patterns and cognitive state (O'Connor et al., 2009; Scanziani and Häusser, 2009).

The strong correlation with behavior suggests that network activity has to mature with increasing behavioral repertoire of an animal or human being. Indeed, at the beginning of life most organisms rely on very few central pattern generators mediating rather simple actions like breathing and feeding. Such vitally important pattern generators are mostly located in deep subcortical structures (Champagnat et al., 2010) while cortical networks are in a very immature state. This is not surprising taking into account that immaturely born animals (like rodents and humans) have relatively little sensory input and a very limited range of typical cortex-related functions like declarative or working memory, complex sensori-motor acts, or behavioral flexibility. Nevertheless, immature networks of the hippocampus and neocortex are electrically active around birth and even in late embryonic stages. This suggests that early network patterns have different functions and underlying mechanisms than mature network-level information processing. Indeed, combined research efforts from many groups have revealed good evidence for a trophic role of early neuronal activity, mediating neuronal survival (Golbs et al., 2011) but also maturation of molecular, cellular, and structural features of cortical circuits (Owens and Kriegstein, 2002; Weissman et al., 2004).

Here, we will review the maturation of coherent cortical activity patterns throughout development. We will briefly describe activity in the hippocampal formation, a three-layered allocortex, and compare it with patterns of typical neocortical areas. Special attention will be then paid to the entorhinal cortex (EC) which forms the anatomical and functional interface between temporal neocortex and hippocampal formation. This region has gained much interest due to its prominent role in spatial navigation and memory formation (Moser et al., 2008) and due to its importance in pathological conditions like Alzheimer's disease (Braak and Braak, 1991; Jellinger et al., 1991). However, the functional maturation of entorhinal networks has been less extensively studied than that of hippocampal or "classical" neocortical areas.

All cortical networks share certain similarities, most prominently the layered structure and, hence, directed and spatially segregated flow of activity. At the cellular level, all cortices share some prevailing types of neurons, e.g. excitatory pyramidal cell with short and long projections and several characteristic types of interneurons. However, they also have marked differences regarding the number and structure of cell layers, internal and external connections, some specific cell types and, notably, developmental time course. Functionally, these commonalities and differences are reflected in some general similarities of early network patterns which, however, differ in many details. While we will highlight several fundamental principles of functional brain development, we will describe typical activity patterns of each area separately. We will also try to guide through the nomenclature of network phenomena in order to avoid confusion about similar terms for different or different terms for similar phenomena, respectively.

2. General principles underlying coherent activity

Coordinated neuronal activity requires structural and functional coupling of neurons. Work during several decades has established various principles of network architecture which mediate synchrony, guarantee appropriate excitation-inhibition balance and sparse coding, and support synaptic plasticity. During recent years, combined efforts from single- and multi-cellular recording, live imaging, field potential recordings and computer simulations have revealed important functional principles which underlie the complex, yet highly ordered temporal patterns within different cortical regions. We will briefly mention the most important principles before discussing specific issues with respect to immature brain tissue.

GABAergic signaling has gained most interest in recent years, owing to the highly powerful and specific role for GABAergic interneurons in orchestrating dynamic pattern formation in neuronal networks (Klausberger and Somogyi, 2008; Mann and Paulsen, 2007; Whittington and Traub, 2003). In fact, the equation of GABAergic signaling with "inhibition" (i.e. reduction in firing probablity) should be abandoned and replaced by the more specific role of GABAergic cells as spatial and temporal organizers of local