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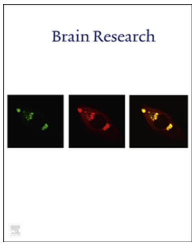

Review

Oscillatory synchrony as a mechanism of attentional processing

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ABSTRACT

The question of how the brain selects which stimuli in our visual field will be given priority to enter into perception, to guide our actions and to form our memories has been a matter of intense research in studies of visual attention. Work in humans and animal models has revealed an extended network of areas involved in the control and maintenance of attention. For many years, imaging studies in humans constituted the main source of a systems level approach, while electrophysiological recordings in non-human primates provided insight into the cellular mechanisms of visual attention. Recent technological advances and the development of sophisticated analytical tools have allowed us to bridge the gap between the two approaches and assess how neuronal ensembles across a distributed network of areas interact in visual attention tasks. A growing body of evidence suggests that oscillatory synchrony plays a crucial role in the selective communication of neuronal populations that encode the attended stimuli. Here, we discuss data from theoretical and electrophysiological studies, with more emphasis on findings from humans and non-human primates that point to the relevance of oscillatory activity and synchrony for attentional processing and behavior. These findings suggest that oscillatory synchrony in specific frequencies reflects the biophysical properties of specific cell types and local circuits and allows the brain to dynamically switch between different spatio-temporal patterns of activity to achieve flexible integration and selective routing of information along selected neuronal populations according to behavioral demands.

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Contents

1. Introduction

Our capacity to process the contents of a visual scene is limited to only a few objects at any given time. Thus, the ability to employ attention in order to select those stimuli or locations that are most relevant for our current goals is critical for our survival. Converging evidence from different experimental approaches has implicated a distributed network of areas in attention and has provided important insights into the role of these areas in the control and maintenance of attention (for reviews see Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000). Moreover, theoretical studies as well as in vivo and in vitro electrophysiology studies have offered a wealth of evidence on the possible cellular mechanisms underlying the selective processing of attended stimuli at the expense of distracters (Desimone and Duncan, 1995; Reynolds and Heeger, 2009).

Methodological limitations, however, for several years, led to a rather restricted view of how the brain achieves a large scale coordination of activity across the extended network of areas participating in attention. On one hand, neuroimaging studies offered a holistic map of activation of the entire brain with limited insight into the temporal modulation of activity across regions. On the other hand, single unit studies in non-human primates provided an account of activity modulations at the single neuron level during attention with unprecedented temporal resolution but poor understanding of the dynamics at the systems level. As a result the question of how spatiotemporal patterns of activity at the level of neuronal ensembles change according to attentional demands remained largely unexplored for several years. In the last two decades, methodological advancements have allowed us to start examining how populations of neurons interact to give rise to behavior. Studies employing large-scale recordings from multiple sites and analytical tools that allow the examination of interactions between activities in distant brain areas have pinpointed oscillatory synchrony as a potential mechanism that boosts sensory representations and promotes effective communication among selected neuronal groups in attention.

Simultaneous multi-site recordings have produced large and complex datasets, which necessitated the development of sophisticated methods of analysis. The dynamic nature of neuronal oscillations and the detailed description of their temporal evolution required an extensive use of time–frequency analyses methods (for a review see Le Van Quyen and Bragin, 2007). Moreover, as data sets become progressively larger, there is an increasing need for the development of robust and sensitive tools that can reveal functional connectivity and directionality of interactions among the distributed nodes of the participating networks (Friston, 2011). Such tools have become freely available to the neuroscientific community and have contributed immensely to a better understanding of the role of oscillatory synchrony in neural processing (e.g. EEGLAB (Delorme and Makeig, 2004); FieldTrip (Oostenveld et al., 2011); Chronux (Mitra and Bokil, 2008); MVGC (Barnett and Seth, 2014)).

The idea that oscillatory synchrony has a functional role for large scale integration of sensory signals was initially proposed by Singer and colleagues as the “binding by synchrony” hypothesis, which aimed to explain how the different features of stimuli are bound to lead to a unified perception of an object (for reviews see Engel and Singer, 2001; Singer and Gray, 1995). This idea led to significant controversy with several studies providing evidence compatible with this hypothesis (e.g. Eckhorn et al., 1988; Engel et al., 1991; Gray et al., 1989) and other against it (Lamme and Spekreijse, 1998; Palanca and DeAngelis, 2005; Thiele and Stoner, 2003). Despite the controversy, these first studies paved the way to the idea that the precise timing of spike occurrence and the temporal structure of activity may have an important functional role in processing of incoming input and could contribute to the emergence of functional networks by gating the flow of information (Salinas and Sejnowski, 2001). Both these functions are critical for attention, which requires the selective processing of signals according to their attentional priority and the selective activation of neuronal ensembles encoding the attended stimulus or location. Although oscillatory synchrony and particularly gamma band synchronization has been associated with a variety of functions (Fries, 2009; Tallon-Baudry, 2009) and has been studied in different species including cats, monkeys, humans, rodents and invertebrates (e.g. Csicsvari et al., 2003; Fries et al., 1997; Siegel et al., 2008; Steinmetz et al., 2000; Wehr and Laurent, 1996), here, we will review findings that link neural