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Inter-hemispheric coherence of neocortical gamma oscillations during sleep and wakefulness

Santiago Castro[a], Matias Cavelli[a], Patricia Vollono[a], Michael H. Chase[b,c], Atilio Falconi[a], Pablo Torterolo[a,*]

[a] Laboratorio de Neurobiología del Sueño, Departamento de Fisiología, Facultad de Medicina, Universidad de la República, Montevideo, Uruguay
[b] WebSciences International, Los Angeles, CA, USA
[c] UCLA School of Medicine, Los Angeles, CA, USA

HIGHLIGHTS

- The electroencephalogram of adult cats was recorded during sleep and wakefulness.
- The inter-hemispheric coherence of the EEG gamma frequency band was analyzed.
- The coherence was larger in alert wakefulness and almost absent during REM sleep.

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ABSTRACT

Oscillations in the gamma frequency band (mainly ≈40 Hz) of the electroencephalogram (EEG) have been involved in the binding of spatially separated but temporally correlated neural events that result in a unified perceptual experience. The extent of these interactions can be examined by means of a mathematical algorithm called "coherence", which reflects the "strength" of functional interactions between cortical areas. As a continuation of a previous study of our group, the present study was conducted to analyze the inter-hemispheric coherence of the EEG gamma frequency band in the cat during alert wakefulness (AW), quiet wakefulness (QW), non-REM (NREM) sleep and REM sleep. Cats were implanted with electrodes in the frontal, parietal and occipital cortices to monitor EEG activity. The degree of coherence in the low (30–45 Hz) and high (60–100 Hz) gamma frequency bands from pairs of EEG recordings was analyzed. A large increase in coherence between all inter-hemispheric cortical regions in the low gamma bands during AW was present compared to the other behavioral states. Furthermore, both low and high gamma coherence between inter-hemispheric heterotopic cortices (different cortical areas of both hemispheres) decreased during REM sleep; this is a pattern that we previously reported between the cortical areas of the same hemisphere (intrahemispheric coherence). In the high gamma band, coherence during REM sleep also decreased compared to the other behavioral states. In contrast, between most of the inter-hemispheric homotopic cortical areas (equivalent or mirror areas of both hemispheres), low gamma coherence was similar during NREM compared to REM sleep. We conclude that in spite of subtle differences between homotopic and heterotopic inter-hemispheric cortices, functional interactions at high frequency decrease during REM sleep.

1. Introduction

Inter-hemispheric communication is achieved by information that is carried by the corpus callosum, anterior commisure and subcortical pathways [1]. Classical split-brain research wherein the corpus callosum is severed has demonstrated that inter-hemispheric communication subserves a large range of behaviors and cognitive functions [16]. For example, recent experiments have pointed out that transient coherent inter-hemispheric coordination underlies functions such as lexical processing [13].

Electroencephalographic (EEG) oscillations in the gamma frequency band (mainly ≈40 Hz) are involved in the integration or binding of spatially separated but temporally correlated neural events. An increase in gamma power typically appears during states/behaviors that are characterized by active cognitive

* Corresponding author at: Facultad de Medicina, Universidad de la República, General Flores 2125, 11800 Montevideo, Uruguay. Tel.: +598 2924 34 14x3234.
E-mail address: ptortero@fmed.edu.uy (P. Torterolo).

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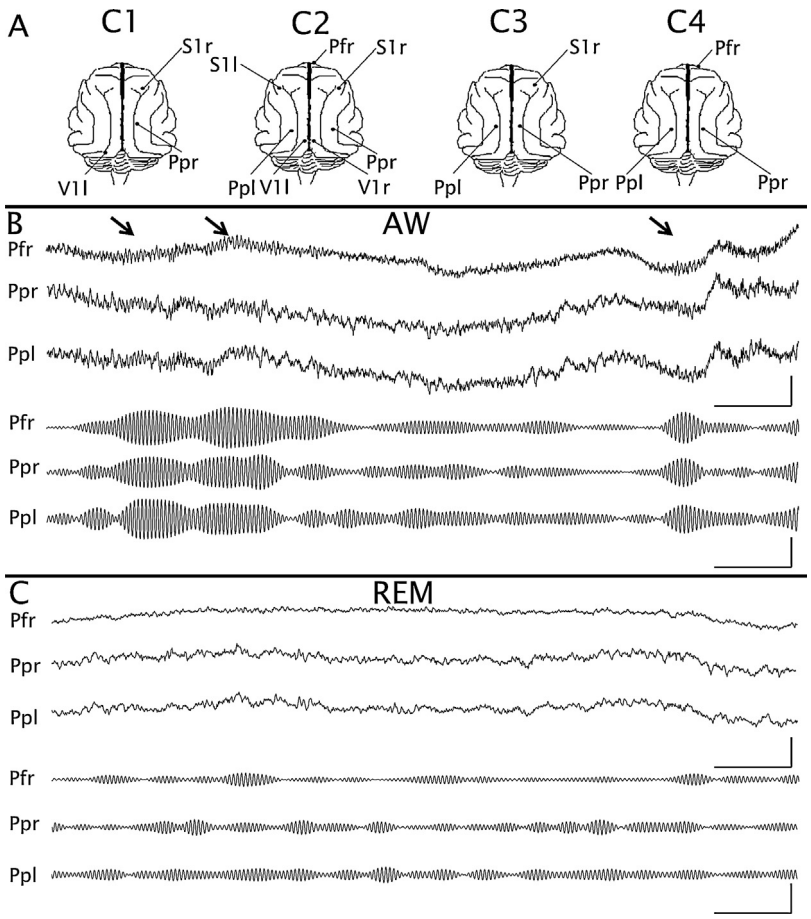

Fig. 1. Gamma oscillations during alert wakefulness and REM sleep. (A) Summary of the position of electrodes on the surface of the primary sensory, association sensory and prefrontal cerebral cortices. These electrodes were referred to a common indifferent electrode, which was located over the frontal sinus. C1–C4, are the animals' names. Pf, prefrontal cortex; Pp, posterior-parietal cortex; S1, somatosensory cortex; V1, visual primary cortex; r, right; l, left. (B) Simultaneous raw and filtered (35–40 Hz) cortical recordings from the right prefrontal (rPf), right posterior-parietal cortex (rPp) and left posterior-parietal cortex (lPp) during alert wakefulness. Gamma oscillations, which are readily observed in the raw recordings (arrows), are highlighted after filtering. Calibration bars: 1 s and 200 μV for raw recordings and 20 μV for filtered recordings. (C) Simultaneous raw and filtered (35–40 Hz) cortical recordings during REM sleep. The amplitude and duration of gamma oscillations decreased compared to alert wakefulness. Calibration bars, as in B.

processing of external percepts or internally generated thoughts and images in humans, and during attentive wakefulness in animals [8,28,29].

The degree of EEG coherence between two cortical regions is believed to reflect the strength of the functional interconnections that occur between them [7]. Coherent EEG activity in the gamma frequency band increases during different behaviors and cognitive functions in both animals and humans [5,6]. In this regard, both gamma activity and gamma coherence between different brain areas has been viewed as a possible neural correlate of consciousness [22].

In the cat, EEG "bursts" of 35–40 Hz oscillations of 200–500 ms and approximately 25 μV can be easily observed in raw EEG recordings ([10] and Fig. 1). Furthermore, EEG intra-hemispheric coherence at 35–40 Hz is greater during alert (AW) than quiet (QW) wakefulness [10]. In addition, intra-hemispheric coherence in the low (35–40 Hz) and high (60–100 Hz) gamma bands decrease to a lower level during non-REM (NREM) sleep, but reaches its nadir during REM sleep. Therefore, during REM sleep, the coupling of high frequency neuronal activity among different cortical areas of the same hemisphere is practically eliminated [10]; comparable results were obtained by other authors utilizing different experimental approaches [9,25,31]. Note that cognitive activities not only occur during wakefulness; dreams, that occur more prominently during rapid eye movement (REM) sleep, are considered a special kind of cognitive activity or proto-consciousness [19].

How is the functional interaction in the gamma frequency band between both hemispheres? Interestingly, a recent study showed that in the condition of corpus callosum agenesia, the gamma coherence (30–55 Hz) did not change during the resting state [18]. However, a subtle increase in gamma band (up to 50 Hz) coherence during REM sleep has been observed in EEG recordings in humans between anterior inter-hemispheric homotopic (equivalent areas of both cerebral hemispheres) leads [2,3]. Consequently, the present study was conducted to determine the interhemispheric coherence in the low (30–45 Hz) and high (60–100 Hz) gamma band between homotopic and heterotopic (different areas of both cerebral hemispheres) cortical areas, during sleep and wakefulness, utilizing the cat as the animal model.

2. Materials and methods

2.1. Experimental animals

Four adult cats (the same as in [10]) were used in this study. The animals were obtained from, and determined to be in good health, by the Institutional Animal Care Facility. All experimental procedures were conducted in accord with the *Guide for the Care and Use of Laboratory Animals* (8th edition, National Academy Press, Washington, DC, 2011) and approved by the Institutional Animal Care Commission. Adequate measures were taken to minimize pain, discomfort or stress of the animals. In addition, all efforts were made in