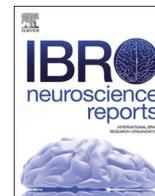


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Research Paper

Stochastic resonance and 'gamma band' synchronization in the human visual system



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A B S T R A C T

Cortical synchronization in the *gamma*-frequency range (above ~ 30.0 Hz) and the signal/noise interplay described by *stochastic resonance* models have been proposed as basic mechanisms in neuronal synchronization and sensory information processing, particularly in vision. Here we report an observation in humans of linear and inverted-U distributions of the electrophysiological (EEG) responses to visual contrast stimulation in the *gamma band* and in the low frequency components of the visual evoked responses (VER), respectively. The combination of linear and inverted-U distributions is described by a *stochastic resonance* model (SR). The observation needs replication in larger subjects' samples. It nevertheless adds to the available evidence of a role of *gamma* oscillatory signals and SR mechanisms in neuronal synchronization and visual processing. Some functional adaptation in human vision appears conceivable and further investigation is warranted.

Introduction

Activated neuronal networks synchronize rhythmically in the *gamma*-frequency range (~ 30.0 – 90.0 Hz). First observed in the visual system and implicated in sensory processing (Eckhorn et al., 1988; Gray et al., 1989; Engel et al., 1991, 1992), *gamma* band synchronization has been posited as a fundamental mode of neuronal activity allowing the transient tuning of neural assemblies and the spatiotemporal accuracy needed in time-related neuronal processes such as perceptual binding, selective attention and memory, cognitive functions (Singer, 1993, 2018; Singer and Gray, 1995; Gray and McCormick, 1996; Sannita, 2000; Buzsáki and Draguhn, 2004; Buzsáki and Wang, 2012; Fries et al., 2007; Bressloff, 2019; Nikolić et al., 2013; Uhlhaas et al., 2010). *Gamma* oscillations recorded at cellular level synchronize over large portions of visual cortex and mediate in the time-dependent activation of the segregated neurons responding to selective stimulus properties (Eckhorn et al., 1988; Gray et al., 1989; Engel et al., 1991, 1992; Singer, 1993; Galuske et al., 2019). The information transfer from retina to visual cortex depends on mechanisms of synchronization comparable to cortico-cortical *gamma* coupling (Todorov et al., 2016). Cortical narrowband *gamma* activity appears selective for contrast visual stimulation and related to the stimulus (grating) spatial frequency (Hermes et al., 2000; Bartoli et al., 2019; Sasaki et al., 2008).

Oscillatory responses *phase-locked* to visual (contrast) stimuli, with frequency centered in the low *gamma* range (~ 20.0 – 45.0 Hz), are recorded in humans by magneto- or electro-encephalographic

techniques as early components of the human broadband visual evoked responses (VERs) and have been suggested to contribute in the development of VERs and in early visual processing. These oscillatory components anticipate those in the VERs lower frequencies (< 20.0 Hz) and have different factor structure and relationship with the stimulus contrast and spatial frequency; they have different cortical source orientations than the VER low frequency components and are recorded in their absence in patients with brain damage impairing visual processing (Sannita, 2005; Sannita et al., 1999; Tzelepi et al., 2000; Bodis-Wollner et al., 2001; Sannita et al., 2007, 2009; De Carli et al., 2001; Narici et al., 2003). In a group of healthy subjects we observed different distributions of the *gamma*- and lower frequency components of the VERs responses that suggest possible functional relationships.

Methods

We analyzed retrospectively (and in full anonymity except for age and stimulation/recording conditions) electrophysiological data previously obtained in a study purported to determine the laboratory standards for individual variability (unpublished). Subjects were acquainted with the recording procedures, laboratory setting and staff and had no evidence or history of ocular, neurological or systemic diseases; their visual acuity was better than 18/20 with optimal correction for the appropriate viewing distance. The electrophysiological retinal (electroretinogram) and cortical (VERs) responses to contrast stimulation recorded according to the International Federation of Clinical

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<https://doi.org/10.1016/j.ibneur.2021.03.001>

Received 13 November 2020; Received in revised form 17 February 2021; Accepted 9 March 2021

Available online 19 March 2021

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Neurophysiology (IFCN) guidelines (Deuschl and Eisen, 1999) were in all cases within normal limits for the laboratory standards. The ethical principles of the Declaration of Helsinki (1964) by the World Medical Association concerning human experimentation were followed. Data were from eleven volunteers (24–37 yr.; mean: 31.3 + 2.6 yr.).

Standard procedures for visual evoked responses recording were applied following the IFCN guidelines for human electrophysiology of vision (Deuschl and Eisen, 1999). The subjects' only commitment during recordings was to focus on the visual contrast stimuli. These were vertically oriented gratings with a sinusoidal profile (5.0 cycles/degree spatial frequency) produced on a Mitsubishi Diamond display by a digital generator (VENUS, Neuroscientific Co., Farmingdale, NY). Stimuli subtended the central 9.0° of visual field at 75 cm viewing distance and were reversed at 2.1 Hz. Mean luminance was 30 cd·m⁻²; contrast was 80%. A fixation point on the screen was provided and the eye position was TV-monitored; single epochs with artifacts due to eye movements were automatically excluded offline. Stimulation was monocular (right eye, reportedly dominant in all subjects). Dermal Ag/AgCl electrodes were positioned 5 cm laterally to theinion and 5% of theinion-to-nasion distance above inion with reference at Fpz and the ground at Cz as indicated by the IFCN guidelines (Deuschl and Eisen, 1999); the electrodes impedance was monitored and proved constant during the recording session. The electroencephalographic signal was continuously recorded; each recording lasted for 29.9 s (with 60 stimulus reversals). The amplifiers (Physio-Amp) bandpass and gain were 0.5–300.0 Hz and 50,000; A/D conversion was at 510 Hz. The digital system generating the stimuli also controlled the electrophysiological data acquisition, which started synchronously with the stimulus onset therefore compensating for the monitor refresh rate.

Twelve recordings were available for each of eight subjects, 13 from two subjects and 21 from one subject. For each subject and each recording, the 500 ms. signal epochs following stimulus reversals were averaged and conventional broadband VERs were obtained. The full-length raw signal was then processed off-line by discrete Fourier transform (DFT), with a 1.03 Hz final resolution, and the amplitude spectrum was computed for each recording. The *gamma* band oscillatory responses were separated from the low frequency components (predominant in the conventional broadband VERs) by a DFT-based digital filter setting to zero all spectral components below cut-off (20.0 Hz) and by averaging the epochs following stimulus onset. Previous work has showed that this

oscillatory response is neither generated by filter distortion nor appears to depend on data acquisition or DFT parameters in these recording conditions (Sannita et al., 1999; Bodis-Wollner et al., 2001; De Carli et al., 2001; Narici et al., 2003) (Fig. 1).

The raw signals were independently analyzed also by a bank of Butterworth filters to obtain a *rectified average* and better characterize the signal frequency/time dynamics. The 1–45 Hz frequency range was partitioned into 19 intervals with 2-Hz width centered from 1 Hz to 39 Hz. For each recording, the *rectified average* was estimated across frequency and time in 1 s windows as the average of the modulus of the amplitude at each frequency interval of the signal. The *rectified average* reflects the activity *phase locked* to the stimulus. The method has been applied to characterize oscillatory signals evoked or induced by sensory inputs in animals and humans; its rationale and mathematical ground are described in detail elsewhere (Salmelin and Hari, 1994; Narici et al., 1998). The values of the *phase-locked* low-frequency VERs components (<20.0 Hz) and *gamma* responses (~ 20.0–40.0 Hz) were computed for each subject and recording in the intervals indicated in Fig. 1 (right).

Results and discussion

Replicable conventional broadband VERs were recorded from all subjects, with latencies and amplitudes compatible with the laboratory normative standards (latency from stimulus of first positive wave: 74.8 ± 8.9 ms.). High pass filtering allowed in all subjects the separation of the oscillatory components in the *gamma* range, always preceding in latency those of the broadband VERs (first positive wave: 56.8 ± 7.9 ms.). The *phase-locked* activity (*rectified average*) in the *gamma* band (~ 20.0–40.0 Hz; amplitude SE within-subject ranging 0.06–0.21) anticipated the activity of the response low frequency components (<20.0 Hz; amplitude SE within-subject: 0.13–0.35) in all subjects. Fig. 1 summarizes the results from one study subject and replicates those of previous normative studies (Sannita, 2005; Sannita et al., 1999, 2009). Ordering from low to high the amplitude values of *gamma* band oscillations *phase-locked* to stimulus (~ 20.0–40.0 Hz) of all recordings resulted in a linear distribution across subjects (R²: 0.926); the distribution of the corresponding values of the low-frequency responses across the scatterplot was better approximated by a non-monotonic, inverted-U function (2° order polynomial; R²: 0.774) (Fig. 2, top). Comparable inverted-U distributions were observed in the entire

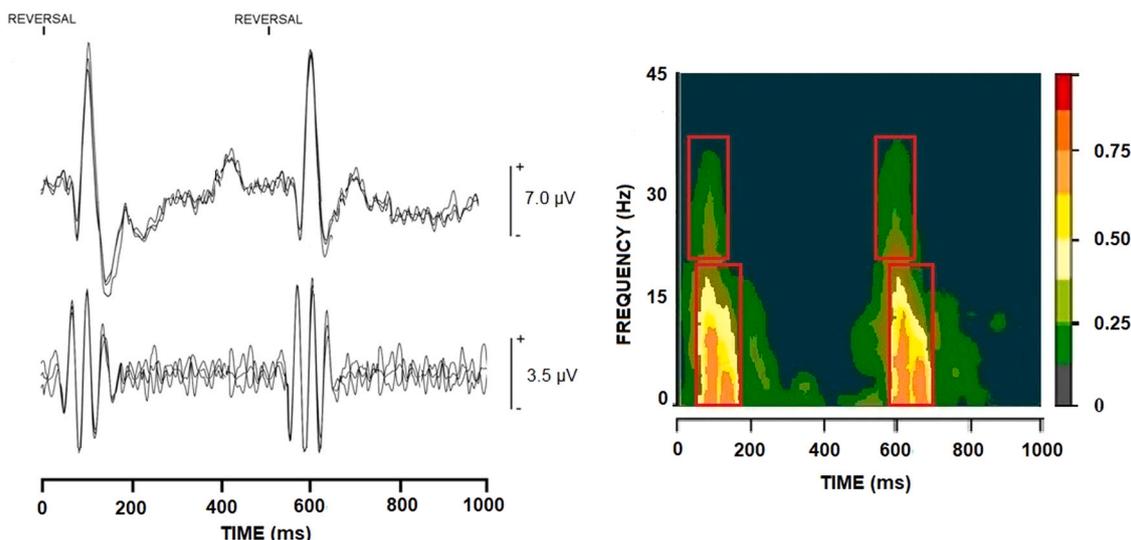


Fig. 1. VERs and *rectified average* obtained from one subject and summarizing the study recordings. LEFT. Superimposed averaged broadband consecutive VERs (0.5–150.0 Hz)(TOP) and oscillatory responses high-pass filtered by DFT (cutoff at 20.0 Hz)(BOTTOM). Right eye stimulation. Reversals of contrast stimuli are indicated by vertical bars. RIGHT. Time/frequency distribution of the signal having a constant time/phase relationship with the stimulus (*rectified average*) from the same subject. Note the clustering of *phase-locked* activity centered at ~20–40 Hz with earlier time dynamics than the activity in the low frequency components of the VERs (<20.0 Hz). These results replicate those from previous studies (Sannita, 2005; Sannita et al., 1999, 2009).

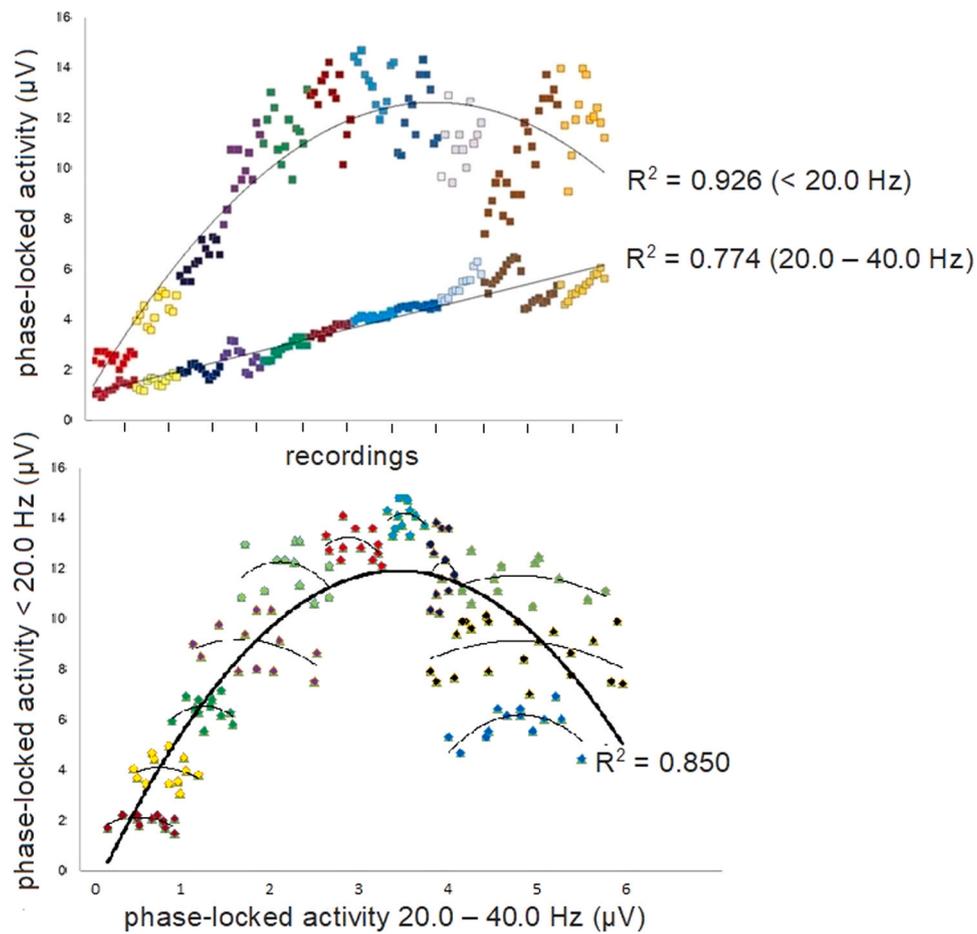


Fig. 2. TOP. Distribution across subjects of the activities *phase-locked* to stimulus in the *gamma* frequency band (20.0–40.0 Hz) ordered from low to highest amplitude and the corresponding values in the VERs low frequency interval (below 20.0 Hz). BOTTOM. Distribution across subjects and for each subject of the activity *phase-locked* to stimulus in the low frequency interval (VERs) vs. the corresponding activities in the *gamma* frequency.

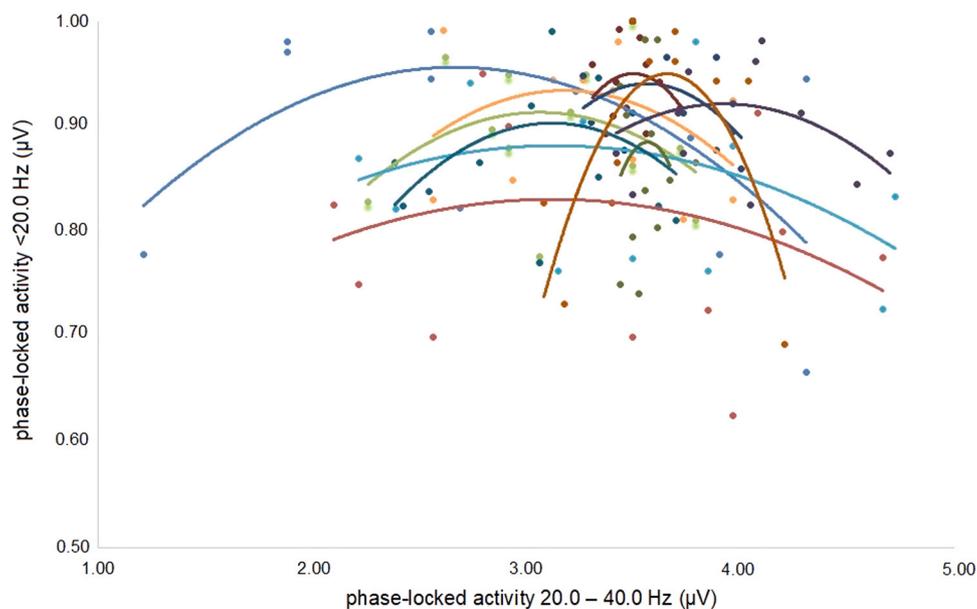


Fig. 3. Distribution for each subject of the activity *phase-locked* to stimulus in the low frequency interval of VERs vs. the corresponding activities in the *gamma* band frequency. Each subject’s values were normalized vs. the subject’s higher power value in the <math>< 20.0</math> Hz frequency range.

subjects' group ($R^2: 0.850$) when each measure of the *phase-locked* activity of low-frequency responses was plotted against the corresponding activity in the *gamma* frequency range (Fig. 2, bottom). Inverted-U distributions were observed for each subject, although with statistical approximation limited by the small sample sizes, but always better than when testing for linear distribution (Fig. 2, bottom: Fig. 3). These observations appear consistent with the evidence from microelectrode studies that low and high frequency electrophysiological signals convey independent information to the visual cortex (Belitski et al., 2008; Mazzoni et al., 2008). The relationship between the distributions of *gamma* oscillations and low-frequency responses appears compatible with a *stochastic resonance* model.

According to theory and experiments, *stochastic resonance* (SR) is a phenomenon with enhanced information transfer and improved detection of signals (if weak and below threshold) when a random or unpredictable interference (usually nicknamed “noise”) is added in optimal amounts in nonlinear (biological or artificial) threshold systems. The system is said to *resonate* at a particular *noise* level in relation to the signal (or system) intrinsic frequencies, thereby improving the *signal-to-noise ratio*. Further increases in the amount of *noise* degrade the signal-to-noise ratio and impair signal detectability (Wiesenfeld and Moss, 1995; McDonnell and Ward, 2011; Moss et al., 2004; Ward, 2002; Ward et al., 2002) for references. Nonlinearity is a common characteristic of neurons and neural networks and *noise* in the nervous system originates from a variety of possible sources (from fluctuations in the neurotransmitter release, number of activated postsynaptic receptors, ion concentrations, membrane conductance, effects of previous action potentials, etc.); synaptic transmission is non-stationary, nonlinear and noisy because of the varying contributions from depolarizing and hyperpolarizing currents; synaptic *noise* affects relatively simple neuronal systems and small amounts of synaptic *noise* from dendritic synapses improve the response to independent, sub-threshold synaptic stimuli in agreement with the SR theory (Poliakov et al., 1996; Traynelis and Jaramillo, 1998; White et al., 2000; Stacey and Durand, 2000; Stocks and Manella, 2001; Linkenkaer-Hansen et al., 2004; Gong et al., 2009; Sejdíć and Lipsitz, 2013); see for references (Wiesenfeld and Moss, 1995; McDonnell and Ward, 2011; Moss et al., 2004; Ward, 2002; Ward et al., 2002). Studies applying psychophysics or magneto- or electroencephalographic techniques have described SR phenomena to occur in the human visual system in a variety of conditions, such as in the perception of sub-threshold gratings, ambiguous figures or letters, three-dimensional perception of autostereograms, and in binocular rivalry, discrimination of motion directions, etc. (Ward, 2002; Ward et al., 2002; Riani and Simonotto 1994; Simonotto et al., 1997, 1999; Speranza et al., 2001; Levi et al., 2005, 2008; Aihara et al., 2008; Sasaki et al., 2008). The addition of white *noise* in proper amounts improves vision in the severely impaired (Itzcovich et al., 2017). Experimental evidence indicates that SR enhances *phase-locking* and promotes synchronization in neuronal systems across many levels of neuronal organization (Sorrentino et al., 2006; Ward et al., 2010; McDonnell et al., 2015). The functional role of *gamma* band activity as information *carrier* has been questioned in favor of its being unstructured noise from neuronal networks (Burns et al., 2011; Xing et al., 2012); some functional role in neuronal synchronization would not be excluded, though. Contributions from unstructured *noise* or a functional interaction between signals would both document the neuronal networks efficiency in benefiting from (intrinsic or artificially added) *noise* and the applicability of SR models in describing these phenomena. In this framework, the inverted-U relationship between *gamma* oscillations and low frequency responses and the signal disruption with higher amplitude *gamma* activity observed in this study are consistent with a threshold SR model, with *gamma* serving as *noise* in some phase of early visual information processing. A model of suprathreshold stochastic resonance, in which small changes in the amount of *noise* improve signals already above threshold, would be particularly applicable (Sasaki et al., 2008; McDonnell et al., 2007; Stocks, 2000).

Gamma activity is ubiquitous in both simple and complex nervous systems, has been observed in a variety of animal species and appears phylogenetically preserved in spite of the increase in size and complexity of mammalian brains (Singer, 2018; Buzsáki and Draguhn, 2004; Buzsáki et al., 2013); SR phenomena have been observed at virtually all levels of neuronal complexity, from neuron membrane to human and animal behavior (Wiesenfeld and Moss, 1995; McDonnell and Ward, 2011; Moss et al., 2004). Some role as robust, basic mechanisms of neuronal function is conceivable for both. The inverted-U distribution observed both across- and within-subject adds to the suitability of SR models in describing basic functions and suggests functional relationships between the *gamma* and low frequency visual responses described by a SR modeling of neuronal synchronization. The observation appears also congruent with the evidence that signal bursts with specific resonant frequencies (depending on subthreshold membrane potential oscillations) cause a postsynaptic cell to fire more than bursts with higher/lower frequencies and mediate in the selective communication between neurons (Izhikevich et al., 2003). Integrated roles of *gamma* activity and SR phenomena seem practicable as the working hypothesis.

Our observation needs replication and systematic research; it only allows inference in this regard and invites speculation. A SR phenomenon should be hypothesized to also reflect (at least to an extent) a functional (visual) adaptation that can be identified in individuals and is also reflected in the variability across subjects. An evolutionary origin (and role) of the interaction between *noise* and sensory information processing in SR models has been suggested but never documented (Wiesenfeld and Moss, 1995); it remains speculative, although selective advantages in survival strategies have been identified in few animal studies (Bahar and Moss, 2004; Dees et al., 2008; Jaramillo and Wiesenfeld, 1998). Operational benefits also in mammal vision are conceivable.

Ethical Statement

All ethical standards have been complied with.

Funding sources

None.

The manuscript has not been published previously in any form, is not under consideration for publication in any other journal, and if accepted will not be published elsewhere in the same form in English or other languages. All authors have equally participated in the study and in the manuscript preparation and agree on the final text.

Conflicts of Interest

To the best of our knowledge there is no conflict of interest to be disclosed.

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