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Mechanisms of Gamma Oscillations
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Supplemental Text

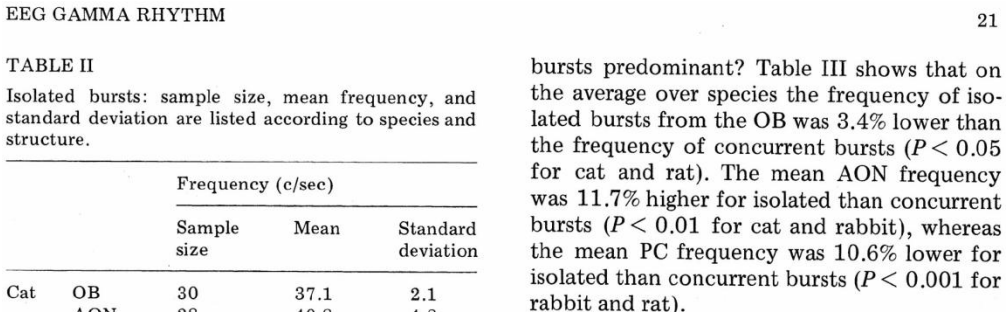
What's in a name? A short history of gamma oscillations

Reconstruction of pieces of neuroscience history is not an easy act, and the origin of the "gamma oscillations" term is no exception. Alpha and beta waves have been introduced by Berger (1929), referring to the larger amplitude rhythmic 8-12 Hz and the lower amplitude faster than 12 Hz patterns, respectively (Niedermeyer and Lopes da Silva, 1993). Perhaps recognizing the different behavioral correlations of different faster rhythms, Jasper and Andrews (1938) used the term "gamma waves" for frequencies between 35 or 45 Hz. The idea that this "40-Hz" oscillation is a "cognitive" rhythm perhaps originates from Henri Gastaut (Das and Gastaut, 1955). The French investigators described high amplitude, 40 Hz rhythmic trains in the scalp EEG of trained yogis during the samadhi state. Banquet (1973) also observed 40-Hz bouts during the third deep stage of transcendental meditation. (For a modern day replication of these observations, see Lutz et al., 2004). In normal subjects, Giannitrapani (1966) found increases in 35-45 Hz immediately prior to answering difficult multiplication questions. Subsequently, Daniel Sheer popularized the "40 Hz" in his many papers on biofeedback (e.g., Sheer, 1966; Bird et al., 1978), which he thought was a higher frequency variant of "beta" waves.

The phrase "gamma rhythm" became popular in the 1980s. According to Walter Freeman "I coined it in 1980, when the popular term was '40 Hz'…At that time Steve Bressler was beginning graduate work in my lab, so I assigned him to a literature search to document the inverse relation of OB [*olfactory bulb, our addition*] frequency and size. Berger had coined alpha. Someone else coined beta (I don't remember who), and Berger coopted it. In analogy to particle physics the next step up would be gamma. I found no prior use of 'gamma' in EEG research, so Steve and I called it that. We sent the manuscript to Mollie Brazier, long-time editor of the EEG Journal. She wrote that she would submit our term to the Nomenclature of the International EEG Society. A month later she reported back that the committee had refused to endorse the usage, so she wouldn't publish it unless we took it out. Steve needed a publication to get support, so we complied. When the article appeared (Bressler and Freeman, 1980), there it was: 'Gamma rhythms in the EEG,' in the running title. I'd forgotten to take it out, and nobody noticed, least of all Mollie. So that's how it first appeared in print. I continued to use it in lectures, insisting that gamma is a range, not a frequency, and it caught on. Now, like numerous successful developments in science, few people know where it came from" (cited from an e-mail correspondence with WF, April 3, 2011).

One of us (GB) received a copy of the originally submitted manuscript from Steve Bressler (he kept it for 30 years!). Indeed, its running title reads "EEG Gamma Waves: Frequency Analysis of Olfactory System EEG in Cat, Rabbit, and Rat". In the Introduction, the authors note that bursts of patterns in the olfactory bulb of various species "was from 35 to 85 Hz, which we propose to call the gamma range" but they acknowledge that "The label 'gamma waves' was used by Jasper and Andrews in 1938 to designate low amplitude beta-like waves at 35-45 Hz in the human EEG, and has been used sporadically again over the following four decades for similar purposes (e.g. Lindsley 1944; Lindsley and Wicke 1974; M. A. B. Brazier, personal communication)". Indeed, in the published version of the Bressler and Freeman paper, the term gamma

oscillation or rhythm cannot be found anywhere, except in the running title (see Figure). Needless to say, that with such an unusual advertisement of the term and without a rigorous definition, gamma rhythm did not catapult to fame instantaneously.



EEG GAMMA RHYTHM 21

TABLE II

Isolated bursts: sample size, mean frequency, and standard deviation are listed according to species and structure.

		Frequency (c/sec)		
		Sample size	Mean	Standard deviation
Cat	OB	30	37.1	2.1

bursts predominant? Table III shows that on the average over species the frequency of isolated bursts from the OB was 3.4% lower than the frequency of concurrent bursts ($P < 0.05$ for cat and rat). The mean AON frequency was 11.7% higher for isolated than concurrent bursts ($P < 0.01$ for cat and rabbit), whereas the mean PC frequency was 10.6% lower for isolated than concurrent bursts ($P < 0.001$ for rabbit and rat).

Although gamma oscillation is most often associated with the "binding" hypothesis, the word gamma is not mentioned in the landmark paper on this topic (Gray et al., 1989). Instead, reference is made several times to "40 Hz" oscillation. This is notable, since Charles Gray was Freeman's graduate student so it is not clear why 40-Hz, instead of gamma, was chosen in the classical account on visual binding nine years after gamma rhythm was re-introduced. As late as 1992, another student of Freeman, Lai-Wo Stan Leung used the term "beta" to describe hippocampal 30-90 Hz oscillations (Leung, 1992).

Despite these subtle inconsistencies in the available information, we suggest to honor Walter Freeman for baptizing 30 to 90 Hz oscillations as gamma band for us. Recently, the term gamma has been expanded to cover higher frequencies (90-140 Hz or even up to 600 Hz; Gaona et al., 2011; Schalk and Leuthardt, 2011), known as "fast" or "high" gamma (Csicsvari et al., 1999; Canolty et al., 2006; Crone et al., 2006). For these higher frequencies Freeman (2007) suggested the Greek letter "epsilon" (å; 80 to 300 Hz), arguing that the mechanisms must be different in this higher frequency range than in gamma. Other terms and frequency bands have been suggested by others, e.g., omega (60-120 Hz), rho range (120-500 Hz) and sigma (500-1000 Hz; Curio, 2000). Unfortunately, both Greek letters rho and sigma (synonymous with thalamocortical spindles) have already been used to refer to sleep rhythms.

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