Spotlight

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Gamma oscillations: precise temporal coordination without a metronome

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Gamma oscillations in the brain should not be conceptualized as a sine wave with constant oscillation frequency. Rather, these oscillations serve to concentrate neuronal discharges to particular phases of the oscillation cycle and thereby provide the substrate for various, functionally relevant synchronization phenomena.

In two recent studies Burns *et al.* [1] and Xing *et al.* [2] investigated the hypothesis that gamma oscillations move through subsequent gamma cycles with constant angular velocity, that is, that the (unwrapped) gamma phase is a linear function of time, even when the time is extended and even if there are short-time phase deviations. By analyzing power spectra in combination with phase scrambling, the authors report convincing evidence to reject the hypothesis. Gamma oscillations do not exhibit sufficient regularity to enable an accurate prediction of gamma phase over multiple oscillation cycles – or as Xing *et al.* [2] put it, gamma oscillations are not a metronome.

This conclusion is correct and in line with numerous previous reports on gamma oscillations. Their analysis documents convincingly what has been known since the beginning of research on gamma oscillations and synchrony. It is a consistent finding that auto- and cross-correlograms show only a handful of side-peaks with decreasing amplitudes [3,4] (but see [5]). Given these results from correlation analyses, Xing *et al.* [2] and Burns *et al.* [1] could not have obtained any other results.

However, we think that the authors err when discussing the implications of their results with respect to current theories concerning the functional role of gamma oscillations. The authors claim that the lack of metronome precision implies that '[t]he prevailing point of view about the timing function of gamma-band activity in perception and cognition needs reevaluation' ([2], p. 13879) and that the results 'call into question theories of gamma activity that claim the gamma band of the LFP may serve as a time-keeping signal' ([1], p. 9662). Thus, they conclude that the current hypotheses about the putative roles of rhythms in the brain fall apart in the light of their findings.

To the best of our knowledge, none of the existing theories about the role of gamma oscillations is based on the assumption that these oscillations are sine waves of one single frequency with phases linearly related to extended time. When presenting their working hypothesis, the authors refer to studies that dealt with the relation between gamma phase and spike timing, but there is no mention in these studies of a metronome function.

Burns *et al.* ([1], p. 9658) write: 'Fries *et al.* (2007) proposed that gamma activity supplies a "temporal reference frame" in which the "precise spike timing" of individual spikes encodes information relative to the consistent phase of gamma activity.' The functions attributed to gamma oscillations in this and the many other studies do not require that the gamma phase unfolds perfectly linearly with extended time. Rather, what matters is the trial-to-trial consistency of spike times relative to the phase of an oscillation cycle: the same stimulus leads predictably to the same phase relation. The empirical findings support this notion: the information content of individual spikes depends on the phase at which they are generated relative to the gamma cycle and phase relationships change dynamically in a stimulus-dependent manner [4,6] (Figure 1).

The hypotheses on the putative functions of gamma oscillations are all based on the ability of membrane potential oscillations to concentrate firing to particular phases of the gamma cycle. This, in turn, can be used to exploit phase space for coding, in order to synchronize discharges of distributed neurons by phase-locking of oscillating cells and to foster communication between neuron groups by phase entrainment [7]. All these functions can be achieved within a few oscillation cycles and do not require a master clock in the form of a 'metronome'. On the contrary, all functional interpretations of these features of temporal coordination assume dynamic changes in phase relations and synchronization on short time scales that need to be realized within a few cycles – and all data available so far support such fast dynamics. This is the case for the relations between gamma synchronization and (i) perceptual organization [5], (ii) brightness perception [3], (iii) communication between cell groups [7], and (iv) attention [8]. Finally, the recent evidence for coding by relative spike timing [4,8,9] can also be fully accounted for by brief gamma bursts, the relevant temporal sequences being in the range of 10 to 20 ms.

One reason that no theory has postulated a metronome function is that gamma oscillations would lose most of their putative functions in cortical processing if their phase unfolded perfectly linearly. If that were the case, the system would enter a one-dimensional limit cycle attractor, which would limit considerably the dimensionality

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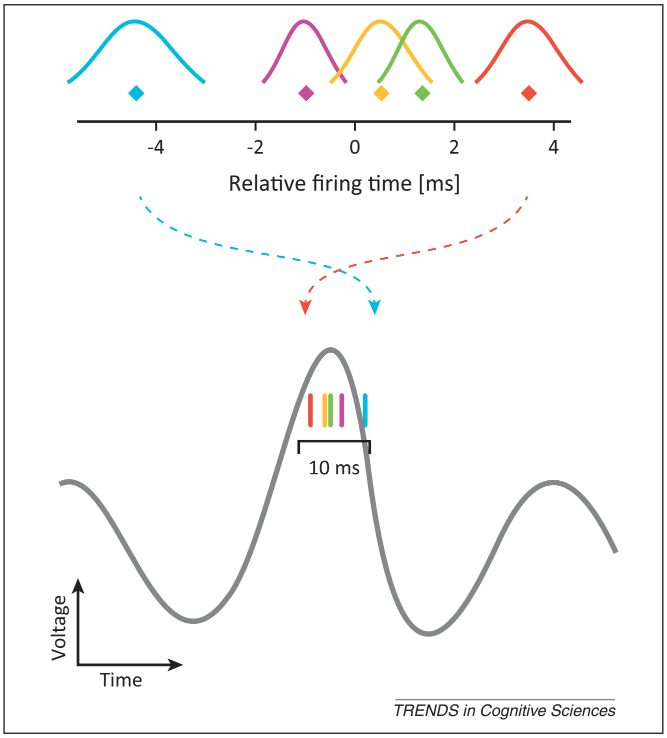

Figure 1. The relationships between the timing of neuronal spiking activity and the phase of oscillation cycle. Top: a sequence in which five neurons preferentially fire for a given stimulus. Bottom: the relationship to the underlying oscillation cycle, as indicated by local field potentials. These relative neuronal firing times are not constant, but change dynamically as a function of stimulus properties (not shown). Reproduced, with permission, from [4].

and flexibility that an adaptive system needs in order to be efficient [10].

In conclusion, we believe that the findings of Burns *et al.* and Xing *et al.* are fully consistent with previous data related to the stability of oscillation frequencies and phase delays in the cerebral cortex. Moreover, in contrast to the opinion expressed by these authors, we propose that their data are also consistent with the presently discussed theories on the possible role of gamma oscillations. Thus, their results do not require a reevaluation of the current views of the function of gamma band activity and associated synchronization phenomena.

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