The gamma wave: a cortical information carrier?

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The perception of visual images as distinct whole entities provides compelling impetus to the search for a correspondingly integral neural substrate for these percepts. In the olfactory system it has been found that odor-specific information is organized as discrete, stable, spatial patterns of neuronal activity in the gamma frequency range (20–80 Hz). The recent discovery of gamma oscillations in visual cortex suggests that a similar mechanism may operate there to integrate preprocessed visual information related to the separate attributes of a single retinal image.

Gamma oscillations in the mammalian brain were first observed in the hedgehog olfactory system nearly 50 years ago. Since then, knowledge of the cellular circuitry and physiology of the olfactory bulb and cortex has greatly expanded. The work of Walter Freeman in particular has demonstrated that oscillatory behavior in these structures is not a property of single neurons, but rather depends on feedback interactions in pools of neurons. In the olfactory bulb, oscillations arise when the populations of excitatory mitral cells and inhibitory granule cells become locked in a negative feedback relation following the onset of inspiration. Mitral cell axonal spike activity and granule cell dendritic potentials manifest gamma oscillations with a phase difference of a quarter of a cycle. Oscillations of the dendritic potential, observable in the extracellular field potential, are spatially coherent, with a common instantaneous frequency across the surface of the olfactory bulb or cortex. Their spatial amplitude patterns contain odor-specific information.

Freeman was the first to report on the visual gamma oscillation in a seminal paper with Bob van Dijk, showing that oscillatory activity in the monkey visual cortex possesses many of the same characteristics as its olfactory counterpart. Charles Gray, coming from Freeman’s laboratory, advanced the field in collaboration with Wolf Singer by the discovery of phase-locking of gamma oscillation between unit activity and local field potentials in the visual cortex of the cat (Fig. 1). Their findings have been confirmed and extended by Reinhard Eckhorn’s group.

Oscillations in the 40–80 Hz range have now been observed in records of single- and multi-unit spike activity and local field potentials in both areas 17 and 18 of the cat. In the case of unit activity, spike-triggered averaging or autocorrelation are used to reveal the rhythmicity. These oscillations exhibit many of the receptive field properties traditionally associated with changes in single-unit firing rate. For example, the oscillations emerge at a recording site in response to specific stimuli in that site’s receptive field, and have orientation tuning curves similar to those based on firing rate. The exact frequency of the oscillation appears to depend not on stimulus orientation, but rather on stimulus velocity.

In those cases where two recording sites (one in area 17 and the other in either 17 or 18) are found to have similar orientation specificity, the appearance of a moving light bar with optimal orientation in their receptive fields produces a marked increase in correlation between their gamma oscillations. Gamma correlation is further enhanced when stimulation is binocular as compared with monocular. These effects do not depend on the mode of activity examined; they are found in single-unit, multi-unit, or local field potential recordings. The stimulus dependence of visual cortex gamma correlations is similar to the enhanced correlation between olfactory bulb and cortex during inhalation as compared with exhalation.

The relation of visual cortex gamma correlations to the integrity of the visual image has been demonstrated in an experiment by Gray et al. In area 17 of the cat, two sites were located, 7 mm apart, which had non-overlapping receptive fields, had similar orientation specificity, and were aligned co-linearly. Gamma correlation between the two sites was measured with three different types of stimulation. Stimulation of the two receptive fields with short light bars at the optimal orientation but moving in opposite directions failed to produce any noticeable correlation between the two multi-unit responses. The gamma oscillations became weakly correlated when the light bars moved in the same direction. Finally, correlation was markedly enhanced when a single long light bar was moved across the two receptive fields. Hence synchronization of gamma oscillations from different locations in visual cortex depends not only on features of the local receptive field, but also on the global integrity of the stimulus.

The Freeman study of monkey cortex provided evidence that spatial patterns of gamma oscillation amplitude contain behaviorally relevant information in the visual system as they do in the olfactory system. It found that oscillatory waves in the 20–40 Hz range occur in coherent spatial patterns over an area of visual cortex greater than 10 cm² and over distances up to 48 mm. The patterns were stable for several weeks, and served reliably to discriminate 100–200 ms epochs representing different stages of processing in the period between a conditioned visual stimulus and a conditioned response. The lower frequency range as compared with that for the cat may reflect a species difference similar to that found for olfaction. The spectral distributions of power for the oscillations were typically broad rather than concentrated at a single frequency, indicating that their source is chaotic rather than sinusoidal.

The concept that emerges from these studies is that information is integrated by a cooperative network of interconnected neurons and is manifested as spatially modulated patterns of synchronized gamma oscillation. If these patterns originate in primary visual cortex, then there must be a means of sharing this information with other cortical areas. The spatial coherence of the oscillations suggests a way in which this may occur. Based on anatomical evidence for convergence of input from patches in area 17 to single
points in other visual cortical areas, one would expect neurons in the target areas to receive axon terminals from projection neurons distributed throughout the area 17 patches. Synchronous oscillations in the spike activities of the area 17 projection neurons would tend to summate and thus be received and integrated by the target neurons, while all asynchronous activity would tend to be cancelled. So the synchronization of gamma oscillations in area 17 could ensure that the oscillation is selectively received in other areas to which area 17 transmits.

Over the past 25 years, Freeman has developed progressively more sophisticated models simulating the generation of oscillatory activity by the interactions and coherent behavior of local populations of olfactory neurons. Other groups are now constructing models for the generation of visual cortex oscillations. As was the case for the olfactory system, theoretical development will depend on basic circuit analysis to determine which cell types interact to produce oscillations, which are excitatory or inhibitory, and which produce spikes or field potentials; it will require physiological measurement of essential visual cortex network parameters such as open-loop time and space constants, and closed-loop feedback strengths.

Finally, the evidence reviewed here casts doubt on the classical description of the human EEG response to light as 'desynchronization'. Because it is highly attenuated owing to volume conduction through the skull, and because its detection is confounded by scalp muscle activity, brain gamma activity is not easily identified in scalp EEG recordings. What appears as desynchronization at the scalp may actually be a shift in synchronization from the alpha frequency range to the higher gamma range. Thus, studies associating event-related 'desynchronization' with attentional processes and those relating gamma activity to focused arousal may be measuring different aspects of a single underlying phenomenon.

It is likely that gamma wave activity will be found in other cortical systems when the pass band of recording amplifiers is set to detect 25. If so, synchronization of gamma oscillations may come to be seen as a general cortical phenomenon, integrating activity among widely separated areas of cortex. The type of interareal coordination that would result has so far only been observed in co-variance patterns of low-frequency, event-related potentials. It may turn out that the gamma oscillation, serving a role as cortical information carrier, is also coordinated in global patterns throughout the entire neocortex.

**Selected references**


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**Fig. 1. Oscilloscope records of multi-unit activity and the local field potential from area 17 in an adult cat.** The onset of the response to presentation of an optimally oriented light bar moving across the receptive field is shown at a slow time scale in the upper two traces. The lower two traces display the activity at the peak of the response at an expanded time scale. The periodic spiking in the multi-unit activity is synchronized with the peak negativity of the local field potential oscillation in the gamma-frequency range. (Adapted, with permission, from Ref. 9.)