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Conférence Analyse d'Images

17h15 – 18h00

Physiological foundations of neurogeometry : the synaptic signature of the "association field" of visual cortical neurons

A prevailing concept in the role of thalamocortical pathways in sensory processing is the dominant influence of feedforward connectivity. In the case of the mammalian visual system, it is well established that topographic maps, the organization of visual receptive fields in ON and OFF discharge zones, and possibly the genesis of orientation selectivity at the cortical level result from the strong imprint of the feedforward input. The spatial convergence of afferents from one relay to the next decides of the functional architecture of the target structure.

The aim of this talk is to examine challenging neurophysiological evidence - based on intracellular recordings in the primary visual cortex *in vivo* - which suggests that visual cortical cells have access to a much wider zone of the visual field than expected from the precision of feedforward projections. I will present evidence showing that a time-window, much longer than previously thought, is available for the primary cortical network to process incoming input through excitatory and inhibitory recurrent and lateral connections, before information is relayed further along the chain of cortical processing. The spatio-temporal synaptic constraints that can be derived from the description of synaptic interaction processes between lateral and feedforward inputs appear to form strong correlates of the "association field" concept derived from Gestalt theory and of perceptual biases measured psychophysically for apparent motion and line motion illusions.

- It is classically accepted that the discharge field of visual cortical neurons is surrounded by a "silent", often suppressive, periphery. Quantitative mapping of subthreshold activity showed that the visually evoked synaptic integration field extends over a much larger area than that established on the basis of spike activity. Surprisingly, point-like stimuli mostly evoke synaptic depolarizing responses which decrease in strength and increase in latency onset at increasing distances from the center of the receptive field (see figure, right panel). Our findings suggest that these subthreshold responses arising from the "silent" surround result from the integration of visual activation waves spread by slowly conducting horizontal axons within primary visual cortex (Bringuier et al., 1999; Chavane et al, 2000).
- Subthreshold depolarizations in area 17 cortical neurons in response to flashed bars can be evoked with onset latencies as early as 18-20 ms whereas the first spike occurrence is generally observed at much longer delays (>35 ms). Our intracellular studies also show the existence of an early shunt signal dominated by GABAa receptor activation often

visible after the start of the initial postsynaptic depolarization (Borg-Graham et al, 1998). Thus a pause of several tens of ms delay exists between the earliest signs of cortical activation and the mean latency of the output V1 signal. Taken into account the slow propagation of visual activity along excitatory and inhibitory lateral connections, one may extrapolate that local inhibitory circuits put the cortical cells "on hold", waiting for the contextual confirmation or invalidation of the relevance of the input by the rest of the network.

- We recently showed that fast apparent motion sequences of collinear Gabor patches, a stimulus known to preferentially activate V1 orientation selective cells, appear for human observers much faster than non-collinear sequences (Georges et al, 2002; Séries et al., 2002). This perceptual bias is most apparent when the feedforward activation produced by the motion signal in the retina travels in phase in the primary visual cortex with the lateral spread of activation. We have investigated synaptic correlates in intracellularly recorded neurons stimulated along the orientation axis with apparent motion sequences of co-aligned or parallel Gabor stimuli, sequentially flashed from surround to center of the recorded discharge field, and from center to surround. Simulations based on psychophysical and physiological data suggest that neural activity spreading through facilitatory and inhibitory long range horizontal intracortical connections modulates the response latencies from V1 neurons to the next incoming feedforward input, thus biasing the response of their MT target neurons and consequently the speed perceived by the human observer.
- Previous anatomical and extracellular studies suggested that horizontal connectivity, intrinsic to the primary visual cortex, preferentially binds neurons with similar orientation preference. I will present correlates between optical imaging studies with voltage sensitive dyes (realized at the Weizman Institute (Jancke et al, 2004; see also figure, left panel) and intracellular recordings (realized at UNIC) aiming at characterizing the dynamics of the visual response produced by an elementary oriented stimulus and measuring its spatial horizontal spread in the primary visual cortex. Optical imaging studies show that iso-orientation selectivity in the propagation pattern appears confined to the feedforward cortical imprint of the stimulated patch of retina. Surprisingly, the cortical territories activated through horizontal connectivity show no particular bias for iso-orientation preference. Iso-orientation preference and tuning selectivity vanish away exponentially with cortical distance beyond a functional hypercolumn dimension (l = 1 mm). In parallel, we used intracellular techniques to directly record synaptic responses evoked by Gabor-oriented visual noise. Electrophysiological results show that visual cortical cells receive a diversity of horizontal synaptic subthreshold input, either tuned with distinct orientation preferences or untuned, which originate from distinct regions of the “silent” periphery of the recorded receptive field. This combined study shows that perceptual bias such as facilitation of collinear visual input and the genesis of “cortical association field” cannot be predicted in a straightforward fashion from the synaptic point-like influence exerted by the intracortical horizontal connectivity. By comparing the propagation patterns produced by composite center-surround oriented stimuli, we conclude that additional cooperative mechanisms linked to spatial and temporal summation, and possibly higher-order cortical feedback, are required. We propose that, similarly to the feedforward input, convergence of horizontal input could initiate the recurrent local cortical connectivity from which propagation of iso-orientation preference could emerge.

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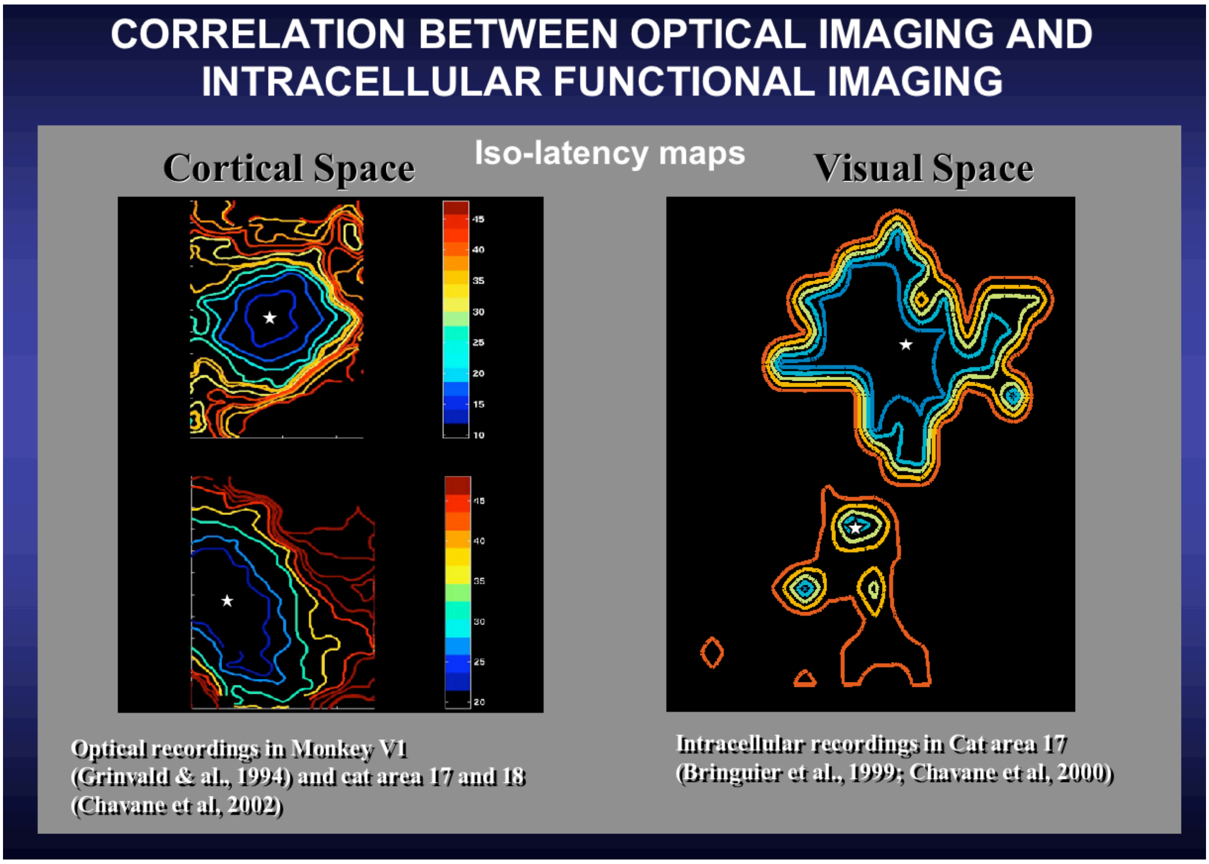
Legend: Dynamics of propagation of the visual activity relayed by the horizontal intracortical connectivity. Left panel: visualization of propagation in cortical space using optical imaging (voltage sensitive dyes: *courtesy from F. Chavane, LNCM & Weizmann Institute).* Colored contours illustrate the cortical location of the front of the propagating wave induced by a point-like oriented input (star) for a given latency (see color code scale expressed in ms). Right panel (UNIC): visualization of the image of the propagating wave across visual space. Each star denotes the location of the discharge field center of each recorded cell. Colored contours code for the stimulus-locked delay of the subthreshold synaptic response recorded intracellularly in a V1 cortical neuron, which increases with the eccentricity of the visual input relative to the discharge field center.



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