Effect of noise on mutually inhibiting pyramidal cells in visual cortex: foundation of stochasticity in bi-stable perception

Naoki Kogo[1], Felix Kern[2], Thomas Nowotny[3], Raymond van Ee[1,4], Richard van Wezel[1], Takeshi Aihara[5]
[1]Biophysics, Donders Institute for Brain, Cognition and Behaviour, Radboud University, The Netherlands
[2]School of Life Sciences, Sussex Neuroscience, University of Sussex, UK
[3]School of Engineering and Informatics, University of Sussex, UK
[4]Brain and Cognition, University of Leuven, Belgium
[5]Graduate School of Brain Sciences, Tamagawa University, Japan

"Bi-stable perception" represents coherent activation of competing signals while their dominance alternates over time. The neural circuit called mutual inhibition (Figure 1) has been assumed to underlie this phenomenon. Each pyramidal cell activates an inhibitory neuron that projects an inhibitory synapse to the competing pyramidal cell, forming disynaptic connections in both directions. It is possible that this circuit exists at various levels of hierarchy in visual cortex and its non-linear responses with dynamic interactions within the hierarchy help to resolve ambiguity of input images due to noise or conflicting information. Therefore, this circuit is highly relevant not only for bi-stable perception but also for emergent properties in perceptual organization in general. However, thorough neurophysiological studies of mutually inhibiting neurons are missing. Recently we established an in vitro neural recording system combined with computerized connections mediated by model neurons and synapses ("dynamic clamp" system). Two (real) pyramidal cells from V1 of mouse visual cortex were recorded by double patch clamp technique while they were connected disynaptically by a mutual inhibition circuit with model inhibitory neurons and model synapses. By depolarizing both pyramidal cells simultaneously, bi-stable activity was evoked: one of the two pyramidal cells became dominant and the other became suppressed and the dominance reversed in time (Figure 2).

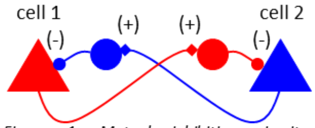

Figure 1. Mutual inhibition circuit. Triangles indicate pyramidal cells and circles indicate inhibitory neurons. The two competing pyramidal cells are mutually connected by disynaptic inhibitory connections.

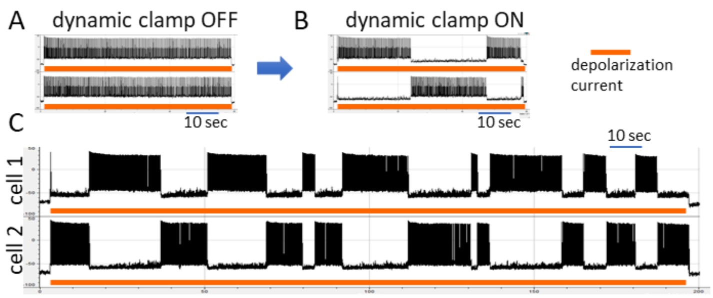

Figure 2. Simultaneous depolarization of two pyramidal cells. A: Without dynamic clamp. B: With mutual inhibition mediated by dynamic clamp. The two neurons showed bi-stability with dominance of activities alternated. C: longer time scale.

Using this system, we investigated the effect of noise on the dynamics of bi-stable activity. In bi-stable perception research, it is known that the histogram of dominant percept durations fits a gamma distribution. This evoked a debate on whether the mechanism of bi-stability is purely a random process or whether it also involves causal processes. Because the dynamic clamp "injects" modeled conductance to the neurons, conductance noise can be given to both the real and modelled neurons. This makes the system an ideal experimental model to investigate the effects of noise on bi-stability. Both excitatory and inhibitory synaptic conductance noise was modelled and given to the pyramidal cells and the inhibitory neurons while the pyramidal cells were exhibiting bi-stable activity (Figure 3 left). The histogram of the dominant activity durations showed gamma-like skewed distributions. The skewedness was enhanced by increasing the standard deviation of the conductance noise and the durations decreased overall (Figure 3 right). Adaptation of the dominant neuron and recovery (from adaptation) of the suppressed neuron caused a decrease and increase of their excitabilities, respectively. In this unbalanced membrane state of the neurons, the fluctuation of membrane potentials due to the given conductance noise appeared to facilitate the reversal. Hence, both, random processes and causal sequences cooperatively contribute to the reversal of dominance in the bi-stable activity we recorded. In conclusion, physiological properties of the circuit, such as adaptation and its recovery, underlying the apparent stochasticity may play a key role in the known causal properties of bi-stable perception such as sequential correlation of percept durations (van Ee, 2009, JOSA) and the stabilization effect by intermittent presentation (Leopold et.al., 2002, Nat. Neurosci.).

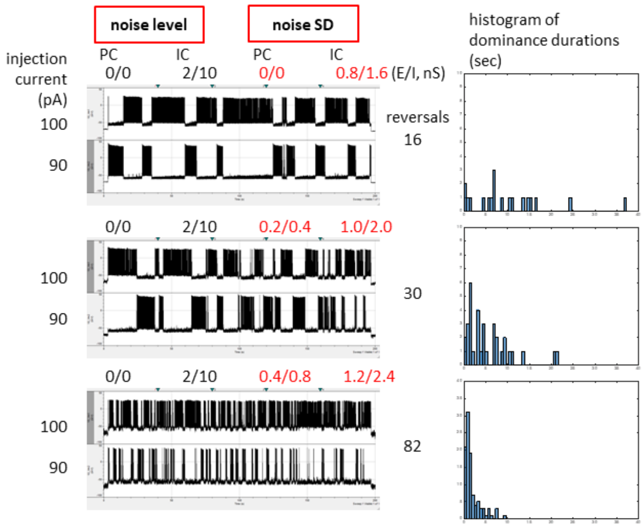

Figure 3. Baseline excitatory (E) and inhibitory (I) synaptic conductance (black values above the plots) was given by the dynamic clamp to both pyramidal (PC) and inhibitory neuron (IC). The standard deviation (SD, red values) of the conductance was systematically changed. Increase of the noise caused skewed distribution of dominance durations.