Chapter 15

Adaptation and Neuronal Network in Visual Cortex

Lyes Bachatene, Vishal Bharmauria and Stéphane Molotchnikoff

Additional information is available at the end of the chapter

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1. Introduction

Complex mechanisms from retina to different visual areas allow us to read these lines. The visual system is inevitable for the way we interact with our surroundings as majority of our impressions, memories, feelings are bound to the visual perception. Millions of cortical neurons are implicated and programmed specifically to frame this incredible interface (perception) for us to interact with the world. Neurons in the visual cortex respond essentially to the variations in luminance occurring within their receptive fields, where each neuron fires maximally by acting as a filter for stimulus features such as orientation, motion, direction and velocity, with an appropriate combination of these properties [1-5].

The seminal work of Hubel and Wiesel on the visual cortex of cat [1, 2, 6-8], has been instrumental in establishing the anatomical and physiological aspects of the visual cortex. Many studies by various investigators on the visual cortex of different animals, thereafter, have been phenomenal in understanding the brain in general and the vision in particular; yet, neuronal mechanisms involved in processing of stimuli still elude our complete understanding of cortical functioning. These findings have been crucial in unravelling the organization of the visual cortex. The visual cortex reorganises itself in the postnatal development, within a specific period called 'the critical period' [9], which is a period characterised with pronounced brain plasticity. In recent years, the focus of the research has been to comprehend the 'reorganization' of neuronal framework, especially after the so called 'critical period' [10-12] in response to various conditions and its ability to adapt accordingly. This amazing tendency of brain to change its neuronal connections and properties is termed 'plasticity' [13]. Two common approaches to study the reorganization of visual cortex are frequently applied: deprivation and induced adaptation. Deprivation refers to the removal of sensory inputs, whereas induced adaptation refers to the forceful application of a sensory input. Consequently, neurons communicate dynamically with each

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other in a specific way self-assembling, auto-calibrating, memorizing and adapting to different stimuli properties, thus responding accordingly to several experiences [14-16].

The aim of this chapter is to primarily focus on how the linkage between cells changes following plastic modifications of cortical neuronal properties, that is, how the reorganization of the cortical network is modulated following adaptation-induced plasticity, as it is inferred by cross-correlating the action potentials of the neurons in the primary visual cortex. We begin with the general architecture of visual cortex (particularly cat visual cortex), followed by a brief introduction to plasticity and adaptation. Then, we cite an example of modification of the neuronal connections before and after adaptation as revealed by cross-correlation method. Based on this example, we propose a model for changing functional connections prior and post adaptation and conclude with how neurons change their functional relationships when forcefully adapted to a non-optimal stimulus.

2. Visual system: Organization

2.1. Introduction

Visual area constitutes about 25 % of the cortex in humans with approximately 5 billion neurons. The study of the visual cortex has revealed many of these visual regions such as V1, V2, V3, V4 and MT on the basis of their anatomical architecture, topography and physiological properties [17, 18]. These regions are involved in processing of multitude of informations (shape, orientation, color, movement, size etc) resulting from the visual pathways, thus making up an image applied to retina.

The cortical area of higher mammals such as cats, monkeys and humans is generally divided into modules of selectivity (e.g. the visual cortex is divided into areas of selectivity called orientation columns). Several characteristics of the visual system of mammals appear to be common to many species [19, 20], though the neurons are distributed in a salt and pepper fashion in the visual cortex of lower animals such as rats and mice, lacking the orientation domains [21, 22]. Research on animal models is used on a large scale to study and investigate the structure and function of the visual system. Monkeys, cats, and mice are commonly used in neurophysiological experiments for understanding cortical mechanisms in general and visual pathways in particular [23].

2.2. From retina to visual areas

Visual perception begins in the retina where the received light is transformed into electrical signal by a biochemical cascade produced in the rods and cones. The retinal ganglion cells relay the message to the lateral geniculate body (LGN) which consists of six layers [24]. Each layer receives information from the retinal hemi-field of one eye. The axon terminals of ganglion cells which project on each layer form a precise retinotopic map. This retinotopy denotes the spatial organization of neuronal responses to visual stimuli. Indeed, in many parts of the brain, neurons that respond to stimulation from a given portion of the visual field are located right next to the neurons whose receptive fields cover adjacent portions.

Therefore, all the neurons in these brain regions form a topographical map of the visual field from its projection onto the retina.

From the LGN, axons are organized into thalamocortical fibres forming the optic radiations. These optic radiations project onto the cortex in specialized visual areas. The distribution of fibres in the cortex can reproduce the visual field on the cortical layer, and the stimulation of a small cortical area leads to the appearance of bright spots called 'phosphenes' [25] in a specific location of the visual field. Visual areas begin in the occipital lobe, and the primary visual cortex or area 17 is the main entrance to cortex for thalamic relay cells [24]. The primary visual cortex is organized into functional modules. Neurons with similar receptive fields are organized into columns [26, 27]. Visual neurons have other fundamental properties, such as the direction selectivity of cells in the layer IVβ, and the selectivity for speed [3, 6]. There is another system of alternating columns, which corresponds to the separation of afferents from both eyes. These are the ocular dominance columns. The ocular dominance columns represent bands of cortical tissue alternately occupied by afferents from the left eye or right eye [28-30]. These bands are particularly pronounced at the cortical layer IV, which receives the afferent endings of the lateral geniculate nucleus. Thus the visual cortex is organized into functional maps of orientation, spatial frequency, ocular dominance, temporal frequency which are interrelated to each other [31-33].

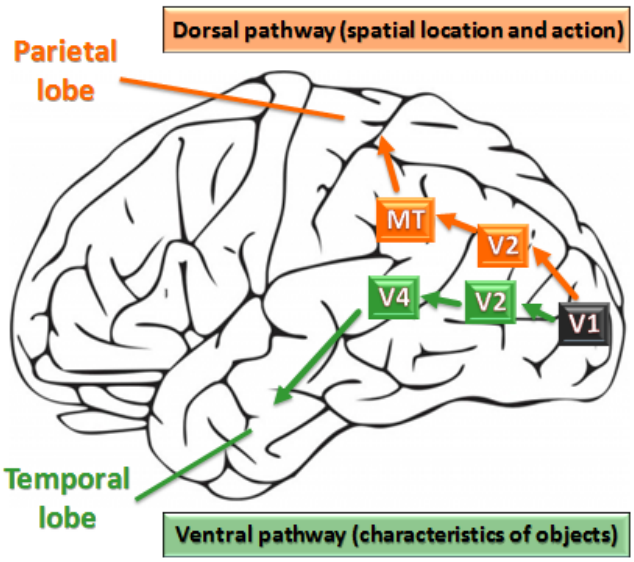

Figure 1. Parallel organization of the visual system

Many findings have led to the discovery of thirty different cortical areas that contribute to visual perception. The primary areas (V1) and secondary areas (V2) are surrounded by many other tertiary or associative visual areas such as V3, V4, V5 (or MT) involved in processing various attributes of trigger features [18, 34]. Areas V3 and V3A are selective to the form of stimuli [35], and neurons of area V4 are selective to colors [36]. Area V5 or MT (middle temporal) is an area where majority of cells are sensitive to motion and direction, and none of which are selective to color [37].

Moreover, the parallel organization of visual system is involved in the establishment of two major visual pathways: Ventral and dorsal pathways which are indispensable for the object recognition [38, 39]. Figure 1 illustrates the parallel organization of visual system, two major pathways: Green part corresponds to the ventral pathway in the cortex ending in the temporal lobe [38, 40]. It is involved in the processing of information on the characteristics of the objects (shapes, colours, materials), that is, object recognition including faces. Orange part corresponds to the dorsal pathway in the cortex ending in the parietal lobe [38, 40]. This path is associated with spatial vision (action / location) of objects, and is involved in processing of action in space.

3. Neuron types in primary visual cortex

3.1. Pyramidal cells and interneurons

The grey matter in the primary visual cortex is divided into six layers namely I, II, III, IV, V, VI (Figure 2) which comprise of different types of neurons [41, 42]. Two types of neurons are mainly observed: pyramidal cells and interneurons which can be physiologically separated and are the focus of interest in this chapter, that is, how they modify their properties and change linkage with each other post-adaptation. Pyramidal cells are excitatory neurons projecting onto other brain regions [43, 44] whereas stellate cells which are the recipient cells from the relay cells of the LGN correspond to the local excitatory interneurons [45]. In addition, there are interneurons that are inhibitory in nature [45]. Figure 2 illustrates the layers and cell types in primary visual cortex. Each layer has specific cell types and connectivity in primary visual cortex. Layer IV contains many stellate cells, small neurons with dendrites arranged radially around the cell body. Pyramidal cells are found in layers II-III, V and VI and are the only type of neurons that send axons outside the cortex. These neurons exhibit two levels of their dendritic extension: basal level close to the cell body and relatively long apical dendritic branches extending sometimes over the entire thickness of the cortex.

Classically, spike waveforms allow cells' distinction into two functional cell-groups, that is, excitatory pyramidal cells and inhibitory interneurons [11, 46, 47]. Figure 3 illustrates a typical example of cells distinguished based on their waveforms: fast spike and regular spike. Figure 3a corresponds to a fast spike with steeper ascending slope of the action potential and represents the putative interneuron [11], whereas Figure 3b corresponds to a regular spike which exhibits a slower ascending slope and represents the putative pyramidal cell [11].

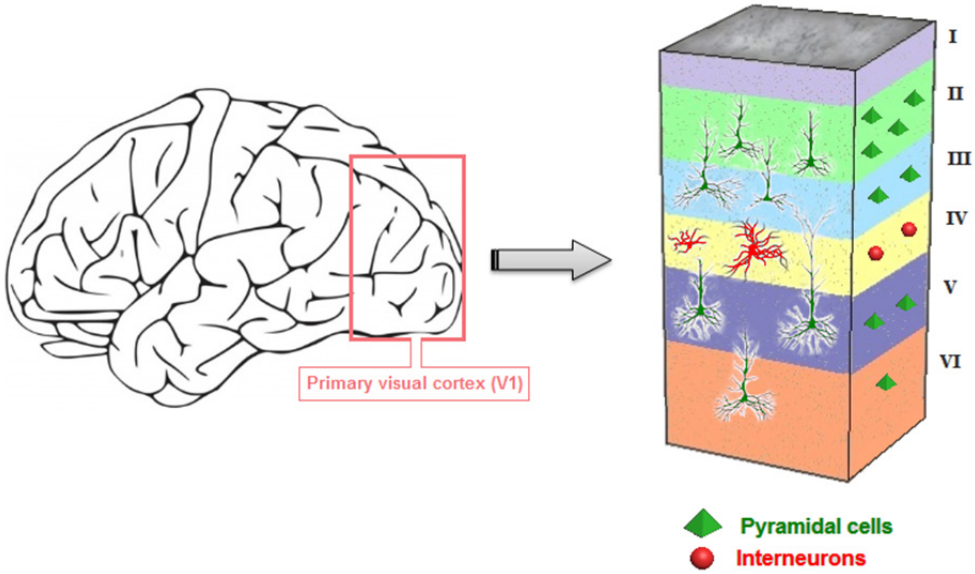

Figure 2. Organization of the primary visual cortex

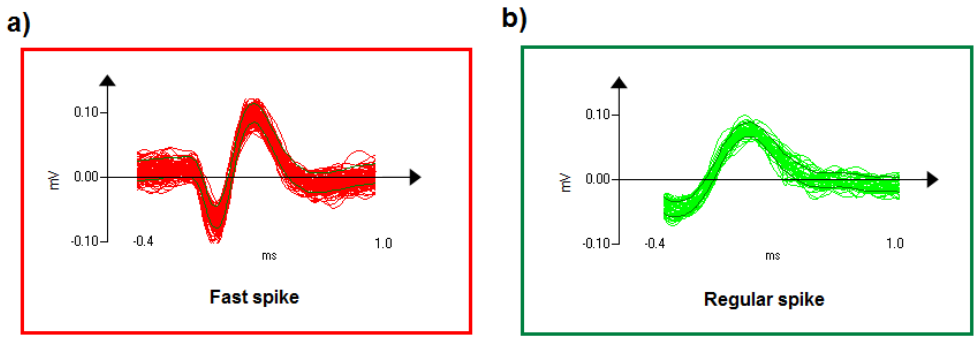

Figure 3. Spike waveforms for putative interneurons (a) and putative pyramidal cells (b)

3.2. Receptive fields

Visual information from the LGN cells firstly projects onto the stellate interneurons in layer IV, which have concentric receptive fields similar to those of LGN neurons [24, 48]. Neurons of layer IV project vertically onto other cortical layers. In layers II / III, cortical cells exhibit a radical transformation of the receptive field organization, where cells respond preferentially to stimuli with properties such as a bar or an edge that has specific characteristics namely orientation, direction, length, width, and motion [3, 6, 49].

Cells in these layers are classified into simple, complex and hypercomplex cells based on their dark or light-edge properties [6]. Simple cell is a cell which has an ON-OFF sub field,

that is, it responds to ON or OFF stimuli in the receptive field and has adjacent excitatory and inhibitory areas [6]. Complex neurons have receptive fields larger than those of simple neurons. They are also selective for orientation, but the precise position of the stimulus within the receptive field is less critical because they have no defined ON or OFF sub-areas. That is why a movement of the stimulus through the receptive field is a potent stimulus for some complex neurons [6, 50, 51]. A complex cell does not have adjacent excitatory and inhibitory areas in the receptive field and responds to whole of the receptive field regardless of the exactitude of the stimulus area, though complex cells can be direction-specific [6]. A hypercomplex cell appears to result, when the axons of complex neurons with different orientations converge on it. A hypercomplex cell is selective to lines of a defined length, and if the stimulus exceeds this length the response is diminished due to inhibitory extremities in addition to antagonistic flanks [6].

Neurons in primary visual cortex are connected laterally and vertically to each other. Lateral or horizontal connections are specified as long range connections between neurons preferring similar stimulus features [52, 53] which are functionally connected to each other at large distance [54, 55]. Vertical connections are specified as inputs to layers II and III from layer IV of the visual cortex [56, 57] which receives its inputs from LGN [58]. From layers II and III, the connections descend to layers V and VI [57].

Cats have a high performance visual system close to that of primates, making it a very coveted subject for researches to reveal the functional aspects of this complex system [59, 60]. Approaches to study the visual system are based on functional electrophysiology, where animals are anaesthetized and paralyzed for electrophysiological recordings by lowering microelectrodes into regions of interest within the visual area and visually stimulating the neurons [6, 11, 49, 61].

4. Plasticity and adaptation in the visual cortex

Neurons in the mammalian visual cortex are tuned to respond to visual stimuli such as contour orientation, motion, direction, and speed [3, 6, 59]. Preference for orientation in orientation columns is considered relatively stable in the primary visual cortex (V1) as an emergent property that is established early in the life, following the so-called critical period [9].

Studies from various laboratories have shown that in a fully mature brain, neuronal network restructures itself beyond the postnatal critical period that follows birth [11, 49, 61-65]. Recent investigations revealed the ability of visual neurons to respond to different stimuli conditions (deprivation or imposition) by changing their optimal properties acquired after birth. This adaptation of neurons for visual perception suggests the existence of neuronal plasticity in adults, hence a mature brain.

Adaptation-induced-plasticity of orientation in primary visual cortex is characterized by authors as the ability of cortical neurons to change their preferred orientation following a long [11, 61, 63] or short [62, 65] exposure to a non-preferred orientation for the primary

visual cortex neurons in cats, e.g. Long adaptation leads to the shift of orientation tuning towards attractive direction [61]. In a similar fashion, repetitive adaptation to a non-preferred spatial frequency reveals the spatial frequency tuning shifts in cat visual cortex [49]. In general, imposing a particular stimulus induces instructive process to modify neuronal properties, for example, when in the visual cortex of awake mice a single orientation grating stimulus is repeatedly presented; it leads to augmentation of responses evoked exclusively by testing stimulus, that is, the experience led to enhancement of response [66]. In experiments where animals are anaesthetized (e.g. a cat in the experiment described later on) the shifts of peaks of tuning curves following adaptation (described in figure 4) are not attributed to attention modulations. Consequently, these shifts result from basic neuronal processes outside the frame of attentional processes that might impact response magnitudes.

Adaptation studies in recent years have presented a more complex picture where prolonged exposure to a non-preferred orientation has shown modifications in neurons' preferred orientations. After adaptation to a non preferred orientation, obtained tuning curve for the new preferred orientation (after adaptation) can shift in two directions relative to the original preferred orientation: attractive or repulsive [11, 61, 63, 64]. An attractive shift is a shift of the tuning curve towards the adapting orientation. On the other hand; a repulsive shift is a shift of the tuning curve in the opposite side of the adapting orientation. Figure 4 illustrates types of shifts post-adaptation. Figure 4a corresponds to an attractive shift, in which blue tuning curve represents control optimal orientation (before adaptation), and red tuning curve represents new optimal orientation (after adaptation).The tuning curve shifted towards the adapting orientation. Figure 4b corresponds to the repulsive shift, in which blue tuning curve represents control optimal orientation (before adaptation), and red tuning curve represents new optimal orientation (after adaptation). The tuning curve shifted away from the adapting orientation. Red arrows depict adapting orientation (non-preferred orientation in control).

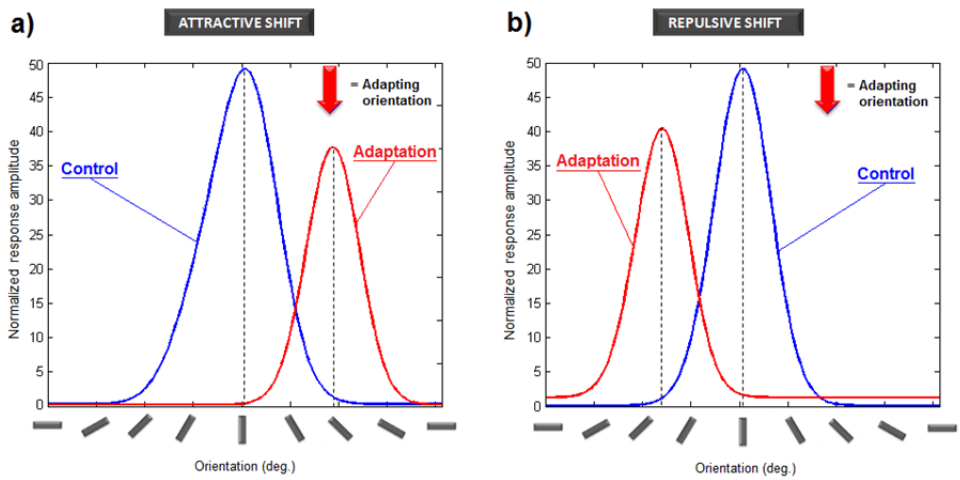

Figure 4. Types of shifts post-adaptation

Attractive shifts are more frequent than repulsive shifts in longer adaptation durations (≥ 6 min) [11, 61]. Repeated or prolonged exposure to an adapter diminished neuronal responses evoked by the original optimal properties, furthermore in parallel, if it is the neuron's preferred stimulus [61]. Optical imaging investigations in recent years have also revealed the impact of adaptation-induced-plasticity, showing that orientation maps in V1 can be modified by imposing one particular orientation [62, 65, 67].

5. Crosscorrelograms and neuronal relationships in visual cortex

As reviewed above [11, 49, 61-65], adaptation- induced studies on visual cortex can reveal a great deal about the functioning of the visual cortex. Crosscorrelogram analysis is an efficient tool to establish the functional connectivity between neurons. Ever since the crosscorrelogram approach was introduced [68], it has proved to be an invaluable tool to determine how specific neurons interact with each other. A crosscorrelogram is a histogram used to infer the connectivity between two neurons, where one neuron is reference and other target. The histogram shows us when the spikes of target neuron are related in time to the spikes of reference neuron. The technique has been instrumental in revealing widespread incidences of neuronal synchrony and neuronal time-relationships among various cortical areas [64, 70-78]. For instance, as revealed by crosscorrelogram analysis, synchrony has been reported to be strong between cells with similar preferred parameters due in part to specific connections between cortical domains having similar tuning properties. Thus, based on the crosscorrelogram analysis, the functional network connections can be established between the neurons [58, 71, 79-81].

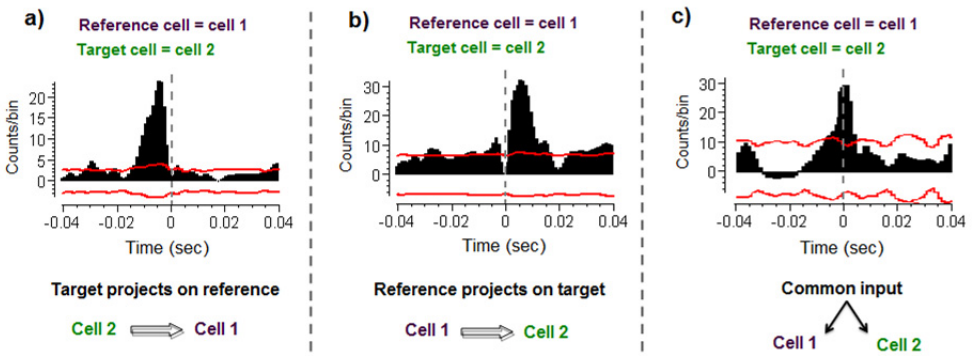

Figure 5. Crosscorrelograms between two neurons (reference and target)

A typical crosscorrelogram between two neurons to interpret the relation between them is obtained by keeping one of the neurons as reference and calculating the spikes of the other neuron with reference to it. An investigator generally is interested in one of the following patterns as illustrated in figure 5, while he is interpreting crosscorrelograms. Figure 5 illustrates the time relations between two neurons as revealed by shifted and corrected

crosscorrelograms when one neuron is reference and other target. A shifted crosscorrelogram is a histogram obtained, when the spikes of the reference cell are shifted by one or two cycles of stimulation. This eliminates the possibility of stimulus-induced-relationship between two neurons. After this the shifted crosscorrelogram is subtracted (corrected) to remove the stimulus-locked -component. Figure 5a corresponds to target cell projecting onto the reference cell. Target neuron fires few milliseconds before the reference cell since the peak of the crosscorrelogram appears few milliseconds before zero, that is, offset from zero, within 5ms. This means there is an excitation from target to the reference cell [79, 81]. Figure 5b corresponds to the reference cell projecting onto the target cell. Target neuron fires few milliseconds after the reference cell since the peak of the crosscorrelogram appears few milliseconds after zero, within 5ms. This means the excitation is from reference cell to the target cell [79, 81]. Figure 5c corresponds to the synchrony between two neurons, as the peak straddles zero [73, 82]. This means there is a common excitatory input to both neurons most likely from other neuron or neurons. Though, various time windows have been taken into consideration ranging from 3ms to 10 ms [72, 79] to reveal the functional connections between the involved neurons, but a time window within 5ms is most frequently used.

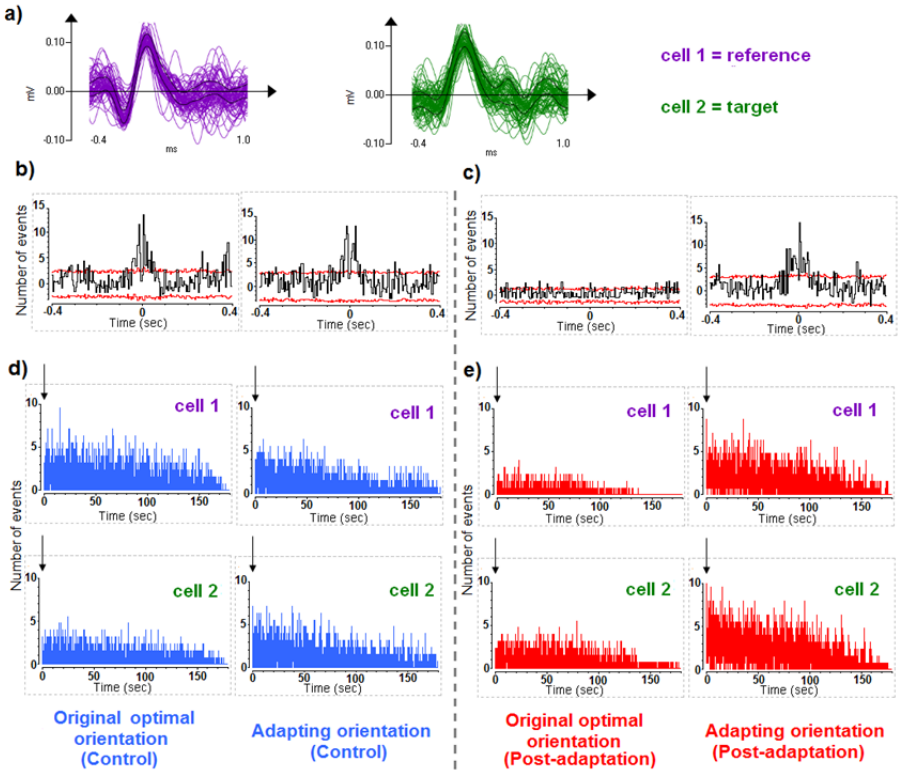

Figure 6. Differential effects of adaptation on synchrony for responses evoked by original orientation and adapting orientation

Figure 6 corresponds to differential effects of adaptation on synchrony for responses evoked by original orientation and adapting orientation. Figure 6a represents respective spike-waveforms for cell 1 and cell 2. Figure 6b shows crosscorrelograms between cell 1 and cell 2 before adaptation (control). The centered peak corresponds to synchrony. Fig 6c represents crosscorrelograms between cell 1 and cell 2 after adaptation. Synchrony disappeared for original optimal orientation while it persists for responses evoked by adapter. Figure 6d shows respective Peri-Stimulus Time Histograms (PSTH's) for cells in control (before adaptation). Figure 6e corresponds to respective Peri-Stimulus Time Histograms (PSTH's) for cells after adaptation. The downward black arrows indicate onset of the drifting sine-wave patch positioned in the receptive field.

Since adaptation modifies the optimal properties of neurons, whether orientation, direction or spatial frequency, it seems reasonable to postulate that these modifications following adaptation induce a rapid reorganization of the inter-neuronal relationships, as revealed by crosscorrelogram analyses. For instance, a recipient neuron programmed since birth to be connected to a specific neuron that responds optimally to one specific property, all of a sudden starts responding optimally to another stimulus, and begins participating in a different network with other neuron- as if breaking its allegiance to the neuron it is programmed to be connected since birth.

6. Network formation

Neurons do not respond in isolation to the trigger features, but in coordination with surrounding neurons. Thus, they encode stimuli features by forming cell assemblies, where in the involved neurons are time related with each other. Recent investigations have revealed the ability of visual neurons to respond to different stimuli conditions by changing their optimal properties acquired after birth. Most of these studies have been done by visual deprivation [9, 83-86], whereas only a few have centered on induced adaptation [11, 62, 64, 87]. This adaptation of neurons to non-optimal stimuli suggests the adaptability of neuronal code to visual stimuli.

Neuronal connections in the cortex generally occur locally [79, 88]. Visual cortex is a highly specialized functional area where the neurons coordinate locally to encode the visual scenes [89, 90, 91]. To reveal how this local circuitry of different neurons in visual cortex is set up and modulated in response to different visual stimuli is of prime importance to understand the mechanisms of information processing. Crosscorrelogram strategy discussed above can be effectively applied to form a neuronal network in response to visual stimuli. Thus, it can be an efficient tool in deciphering the changes in the neuronal code post-adaptation, hence, the mechanisms of plastic modifications can be revealed.

For example, in the Figure 7 we show the network of connections prior and post adaptation between three neurons recorded simultaneously from the same electrode lowered into the primary visual cortex of an anaesthetized cat. In this experiment, a stimulating sine-wave drifting grating was set to excite cells optimally. Shifted and corrected crosscorrlegrams

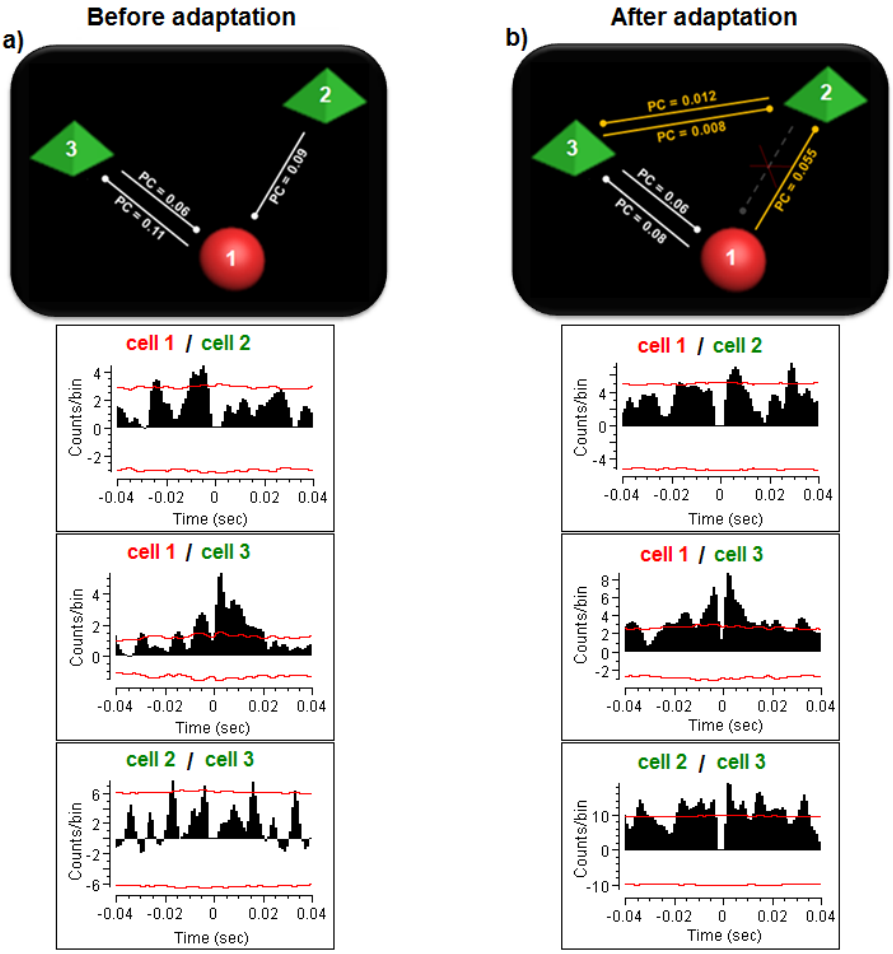

Figure 7. Functional relationships between simultaneously recorded cells before and after adaptation

between all the involved neurons were obtained. A time window of 5 ms before or after the zero in the shifted and corrected crosscorrelogram is taken into account for the projection to be valid. The physiological connectivity (synaptic connections, common input) between cells occurs on very small time scales, less than 3 ms [79, 81]. Since we consider a time window of 10 ms in crosscorrelograms for establishing connections, therefore, this connectivity only reflects that the cells function (irrespective of physical connectivity) in coordination with each other in a time-window of 10 ms following a presented stimulus. Figure 7a illustrates the functional connections between three neurons as revealed by their respective crosscorrelograms (shifted and corrected). White projections correspond to established connections before adaptation. Figure 7b illustrates the new functional connections between same neurons as revealed by their respective crosscorrelograms (shifted and corrected). Yellow projection corresponds to the new connection established after adaptation. Dotted

gray projection represents the disappeared projection. PC corresponds to the probability coefficient of the connections. Solid green pyramid represents a pyramidal cell and the solid red sphere represents an interneuron. Red curve line indicates 95% significance level.

This changing of connections indicates that the functional relationships between neurons are modified depending on the stimulus features. For instance, following the forceful presentation of a particular stimulus (in this example a different orientation) results in disappearance of some relationships, and appearance of new relationships.

Based on the above example, we hypothesize and propose a model how the network of neurons is modulated prior and post adaptation as revealed by the functional time-relationship of neurons between them. Figure 8 depicts the functional connections between the same neurons before and after adaptation. White projections in figure 8a show the projections that cells have onto each other before adaptation, whereas figure 8b depicts how the network changes in the same group of neurons after adaptation. Some of the connections between the cells remain distinct (white projections) whereas some connections disappear (dotted gray arrows) with appearing new connections (yellow projections).

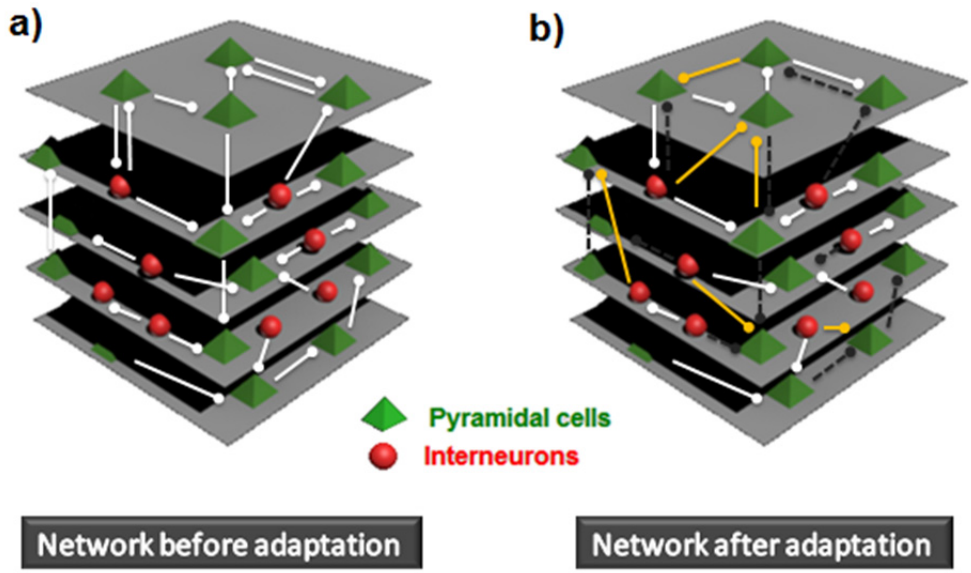

Figure 8. Network model before and after adaptation

7. Conclusion

This chapter reviewed the changes in the cellular properties post-adaptation. Indeed, the optimal trigger features may change following the prolonged application of a stimulus to which the cell responded feebly before adaptation. This phenomenon has been virtually observed in all mammals which have been tested so far. Also in parallel, following

adaptation the inter-neuronal relationships are modified. This suggests that the entire cortical network reorganises itself post adaptation, that is, a new cortex is formed, as if designed for changed properties.

To sum it up, it is of prime importance to understand the plastic modifications of brain for various fundamental and medical reasons. This chapter underlined the importance of imposed adaptation studies within brain, particularly in primary visual cortex based on the crosscorrelogram analysis, framing a premise to better understand the functional connectivity [79, 92] and mechanisms in local neuronal circuits between various identified neurons, at least between the pyramidal cells and interneurons before and after adaptation. and post adaptation, thus, could help us to decipher the mechanisms of information processing, hence the neuronal codes governing them.

Author details

Lyes Bachatene* and Vishal Bharmauria*
Department of Biological Sciences, University of Montreal, Montreal, Canada

Stéphane Molotchnikoff**
Department of Biological Sciences, University of Montreal, Montreal, Canada

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* Both Authors Contributed Equally
** Corresponding Author

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