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Current Opinion in Neurobiology

Cell Types, Circuits, Computation

Rava Azeredo da Silveira[1,2] and Botond Roska[3]

How does the connectivity of a neuronal circuit, together with the individual properties of the cell types that take part in it, result in a given computation? We examine this question in the context of retinal circuits. We suggest that the retina can be viewed as a parallel assemblage of many small computational devices, highly stereotypical and task-specific circuits afferent to a given ganglion cell type, and we discuss some rules that govern computation in these devices. Multi-device processing in retina poses conceptual problems when it is contrasted with cortical processing. We lay out open questions both on processing in retinal circuits and on implications for cortical processing of retinal inputs.

Addresses
[1] Department of Physics and Department of Cognitive Studies, École Normale Supérieure, Paris, France
[2] Laboratoire de Physique Statistique, Centre National de la Recherche Scientifique, Université Pierre et Marie Curie, Université Denis Diderot, France
[3] Neural Circuit Laboratories, Friedrich Miescher Institute for Biomedical Research, Basel, Switzerland

Corresponding authors: Azeredo da Silveira, Rava (rava@ens.fr) and Roska, Botond (botond.roska@fmi.ch)

Current Opinion in Neurobiology 2011, **21**:664–671

This review comes from a themed issue on
Networks, Circuits and Computation
Edited by Peter Dayan, Dan Feldman, Marla Feller

Available online 9th June 2011

0959-4388/$ – see front matter
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DOI 10.1016/j.conb.2011.05.007

Introduction

The mammalian brain is assembled from thousands of neuronal cell types [1], organized into distinct circuits that perform computations relevant to behavior. Sophisticated local circuits exist in all brain regions and they act in concert in the behaving animal. In order to gain mechanistic insights into brain function, it is crucial to uncover *what* these local circuits are computing and *how* computations are achieved. Furthermore, understanding the changes that occur in those neuronal circuits involved in specific brain diseases may help design strategies for therapy. One of the most intriguing questions about local neuronal circuits pertains to the relation between structure and function: How does the connectivity of a circuit, together with the individual properties of the cell types that take part in it, result in a given computation? Here, we review recent developments, which begin to answer this question, in examples of mammalian retinal circuits in which structure and function can be approached by means of genetic tools as well as by imaging and physiological techniques.

The retina as a model system

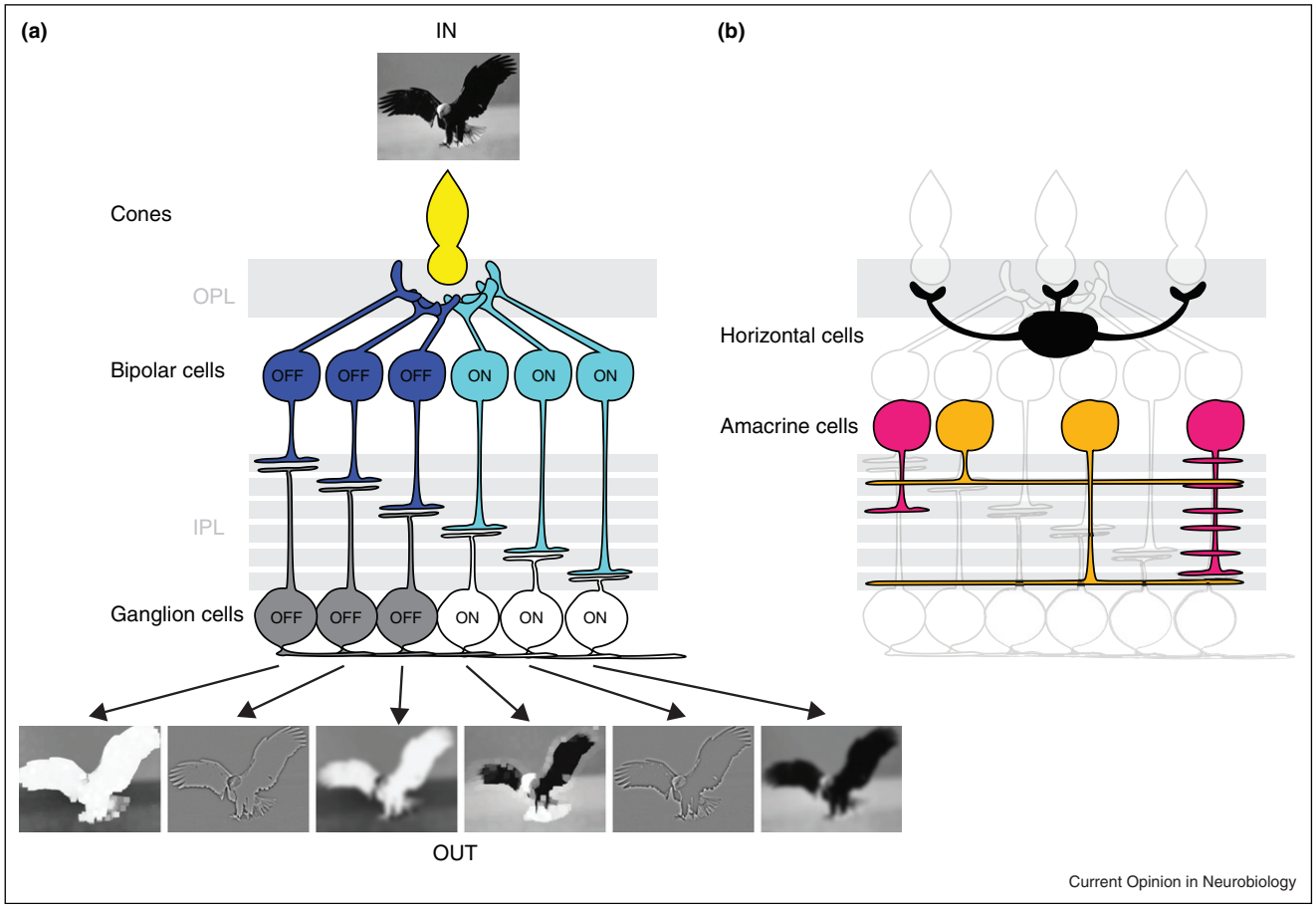
The first steps of visual processing take place in the retina [2,3], which also serves as a unique model system to study the relationship between structure and function. The retina is a self-contained system in the sense that, if the retina is involved in a particular neuronal computation, then one can understand the mechanisms of this computation through the study of retinal circuits alone. This is owing to the fact that, unlike fish [4] and bird [5], mammals have minimal feedback from higher brain centers that possibly carries only modulatory commands [4]. It is easy to isolate and maintain a healthy retina *in vitro*, and its natural inputs, dynamically evolving light patterns, can be presented to it in a controlled and quantitative manner. In probing the retina, neuronal activity from any cell class can be recorded.

In the past few decades, many investigations [2,3] have pointed to the existence of specialized cell types and have found that these cell types are organized in local circuits. Cell types and circuits are ordered in neuronal layers in the retina (Figure 1), which greatly simplifies the study of connectivity between neurons. The emerging picture is that each retinal output neuron, a ganglion cell, of a given type has an afferent circuit in which a few other cell types take part. Ganglion cell types are arranged in mosaics [2,3] (Figure 2), with various degrees of overlap between the dendritic fields of the individual cells of the same type.

The 'what' and the 'how' of retinal computation

Recent work from several groups suggests that the retina acts as the sum of many small devices – the circuits of different ganglion cell types – each highly stereotypical and task-specific [7,8••,9,10••,11••,12–16]. It appears that an appreciable fraction of these circuits is devoted to the analysis of different categories of motion. Eight types of direction-selective ganglion cells (four ON–OFF types [14,17–19], three ON types [14,18], and one OFF type [10••]) report either the direction of lateral object motion or the direction of global image drift. Approach motion is detected by at least one ganglion cell type [11••] and other ganglion cell types respond to differential motion relative to global background motion [12]. In all three cases of motion sensitivity – direction selectivity, approach sensitivity, and differential-motion sensitivity – the ganglion cells respond most vigorously to a so-called preferred

Figure 1



Functional organization of the mammalian retina. **(a)** The retina can be viewed as a parallel image processor that acquires movies (top panel) with its array of photoreceptors, and uses its internal circuits to compute dozens [2,3,6] of different neuronal representations (bottom panels) of the visual world. These are sent to higher brain centers via axons of the ganglion cells. Cone photoreceptors (middle panel, yellow), which are the light sensors in daylight, connect to about ten types of bipolar cells. Half of the cone bipolar cells are activated by decrease (OFF cells, blue) and the other half by increase (ON cells, cyan) in light intensity. Axon terminals of OFF and ON bipolar cells settle at different depths within the inner plexiform layer (IPL): OFF terminals in the distal part and ON terminals proximally. Order exists at an even finer scale: bipolar cell terminals occupy one or a few of IPL strata (horizontal gray bars in the IPL). Dendrites of more than a dozen types of ganglion cells arborize in these strata and receive excitatory input from co-stratified bipolar cell terminals. The response polarity of a ganglion cell is determined by the types of bipolar cells that provide input to it: ON (white), OFF (gray) or ON–OFF. **(b)** The photoreceptor-to-bipolar synapse in the outer plexiform layer (OPL, top gray horizontal bar) is regulated by inhibitory horizontal cells (black). Similarly, excitatory synapses between bipolar and ganglion cells are modulated by inhibitory amacrine cells. These cells receive excitatory input from bipolar cells, and they provide feedback and feedforward signals to bipolar terminals and ganglion cell dendrites respectively. Amacrine cells are the most diverse of the retinal cells: more than 30 morphological types have been described [2]. As yet, the functions of most of them are unknown. Amacrine cells are either GABAergic or glycinergic. GABA-releasing cells have long processes and are therefore called wide-field cells. Glycine-releasing cells have short processes, which often span several strata; these cells are often referred to as narrow-field cells. This architecture is further enriched by amacrine–amacrine cell inhibitory connections and by various electrical synapses within and among cell types.

stimulus, while their responses to so-called null stimuli are suppressed. In the case of the three motion categories, the preferred stimuli are lateral motion in a given direction, approach motion, and spatially differential motion, respectively, whereas null stimuli are lateral motion in the opposite direction, receding and lateral motion, and coherent whole-field motion, respectively. Yet another type of motion sensitivity consists in the suppression of response, in a few ganglion cell types, to the rapid image shifts [13] that occur during wide-angle, fast eye movements, the so-called saccades. Here the null stimulus, global image motion, is similar to that of the differential-motion sensitive cells, except that a high speed of global motion is required.

It is important to note that in general ganglion cells are broadly tuned: 'sensitivity' does not mean 'exclusivity'. Indeed, motion-sensitive cells do not respond *only* to their preferred stimulus. For example, an OFF direction-selective, approach-sensitive, or differential motion-sensitive cell will respond vigorously to a dark flash, like any other OFF ganglion cell. The essence of motion

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