

Spikes and ribbon synapses in early vision

Tom Baden¹, Thomas Euler¹, Matti Weckström², and Leon Lagnado^{3,4}

¹ Centre for Integrative Neuroscience, Bernstein Centre for Computational Neuroscience (BCCN), Institute for Ophthalmic Research, University of Tübingen, Tübingen, Germany

² Department of Physics, University of Oulu, Oulu, Finland

³ Medical Research Council (MRC) Laboratory for Molecular Biology, University of Cambridge, Hills Road, Cambridge, UK

⁴ School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

Image processing begins in the retina, where neurons respond with graded voltage changes that must be converted into spikes. This conversion from ‘analog’ to ‘digital’ coding is a fundamental transformation carried out by the visual system, but the mechanisms are still not well understood. Recent work demonstrates that, in vertebrates, graded-to-spiking conversion of the visual signal begins in the axonal system of bipolar cells (BCs), which transmit visual information through ribbon-type synapses specialized for responding to graded voltage signals. Here, we explore the evidence for and against the idea that ribbon synapses also transmit digital information. We then discuss the potential costs and benefits of digitization at different stages of visual pathways in vertebrates and invertebrates.

Introduction

Sensory systems encode physical stimuli that vary continuously, such as the loudness or frequency of sound or the intensity of light. The receptor cells that sense these forms of energy represent the intensity of the stimulus through changes in membrane potential, an analog representation that varies as a continuous function of stimulus amplitude. The subsequent transmission of this information to the brain typically requires this analog signal to undergo a fundamental transformation: digitization into action potentials (APs or spikes, see [Glossary](#)). The amplitude of APs is relatively fixed; thus, information is mainly contained in their temporal sequence. The necessity for digitization arises from fundamental properties of neuronal signal conduction. Left to spread passively, graded voltage signals rapidly become smaller and slower as they move from their point of origin. By contrast, APs involve regenerative mechanisms, allowing signals to be transmitted along axons over large distances while maintaining reliability and temporal precision.

Analog-to-digital (A–D) conversion occurs at different stages of pathways for different sensory modalities ([Figure 1](#)). Some primary receptors can immediately generate spikes for transmission through their long axons,

such as mechanoreceptors in the skin and olfactory receptors in the nasal epithelium. Other mechanosensitive neurons, such as hair cells of vertebrate auditory and vestibular systems, generate analog signals that are only transmitted as far as a synapse located in the main cellular compartment, with A–D conversion occurring in the secondary afferent neuron. Why should different sensory systems carry out A–D conversion at different stages? How does this conversion occur and what is it good for? How are the synapses that transmit these signals suited to their task? In this review, we discuss these questions by making comparisons between the early visual system of vertebrates and insects.

Circuits carrying out the first stages of visual processing

The vertebrate retina is the window of the brain onto the visual world and a beautiful neural circuit [1,2]. Here, photoreceptors (PRs) convert light into graded changes in membrane potential for transmission to secondary neurons, the retinal BCs, through ribbon synapses. BCs in turn form excitatory connections with retinal ganglion cells (RGCs), which deliver the results of retinal processing to the brain as a spike code. At each synaptic stage of this vertical pathway, visual signals are shaped and modulated by complex interactions with inhibitory interneurons: horizontal cells in the outer retina and amacrine cells (ACs) in the inner retina. Notably, several AC types also respond to visual stimuli with regenerative depolarizations, including

Glossary

Action potential (AP): a highly stereotypic, all-or-nothing depolarizing voltage transient, with a clear refractory period, driven predominantly by sodium influx, as used by most neurons and described by the Hodgkin–Huxley model.

Damped voltage oscillation: an electrical resonance generated by the balanced interplay of voltage-activated inward and outward currents, for example, mediated by calcium and potassium channels. Imbalance of the currents either suppresses the oscillation, or converts depolarizing phases into spikes.

Digital signals: voltages that have near-constant amplitude and are clocked with a certain speed (cycles/s). Used here as shorthand to depict pulse trains of voltages in the form of APs.

Rebound spike: a single spike elicited after release from (strong) hyperpolarization.

Spike: we use ‘spike’ as a collective term to denote a stereotypic, fast regenerative depolarizing voltage transient with a clear voltage threshold that is supported by either sodium and/or calcium currents. ‘Spikes’ include both APs and spikelets.

Spikelet: a spikelet can have variable amplitudes and is supported by either calcium and/or sodium currents.

Corresponding author: Baden, T. (Thomas.Baden@uni-tuebingen.de).

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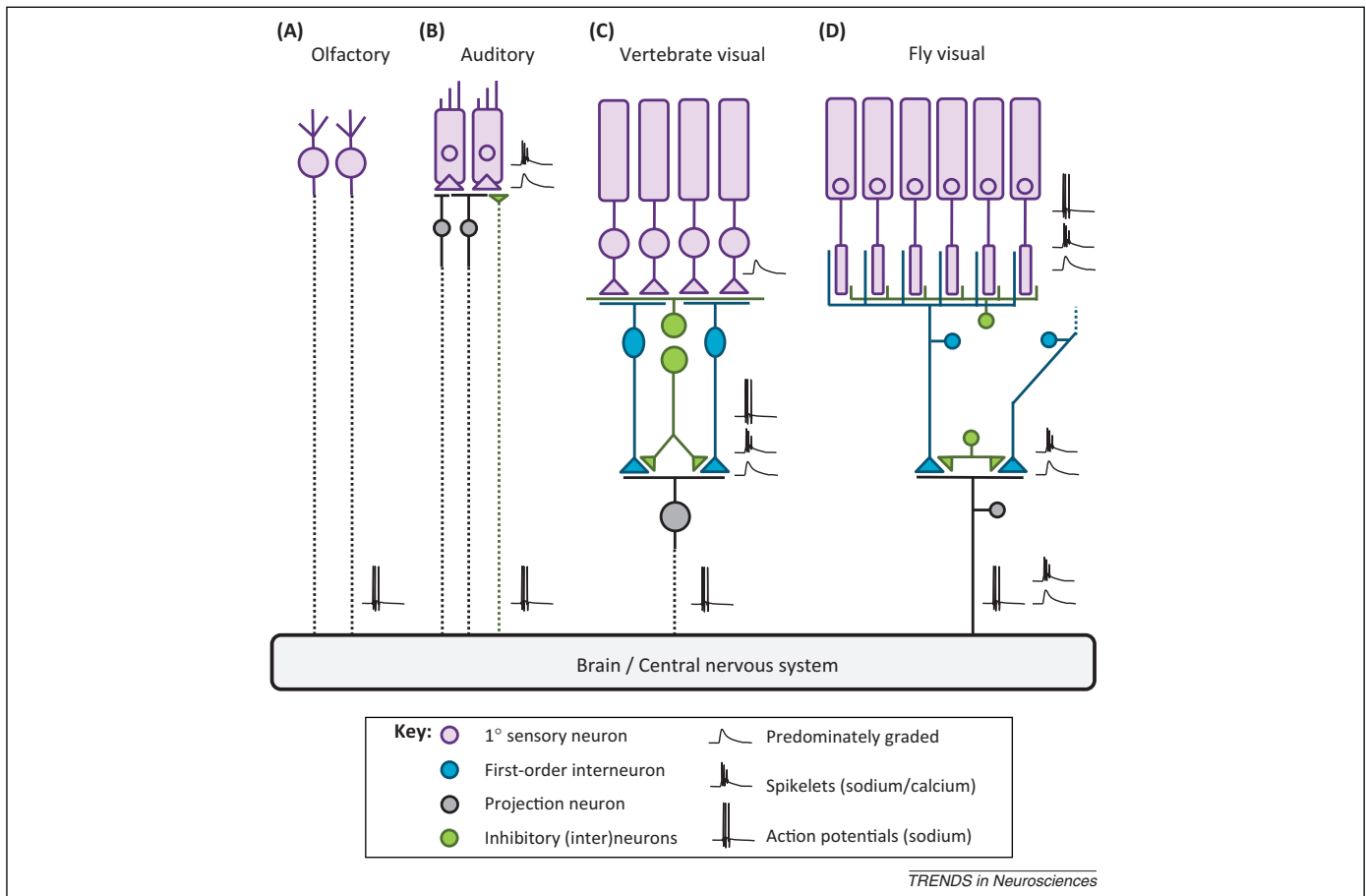


Figure 1. Analog–digital (A–D) conversion in different sensory systems. Different sensory systems implement A–D conversion at different processing stages. **(A)** Olfactory receptor neurons feature long axons that generate spikes themselves. **(B)** Hair cells forward a graded and/or spiking signal to spiking afferents and, depending on the system, they can receive efferent inhibition. **(C)** In the early vertebrate visual system, photoreceptors (PRs) forward visual information via bipolar cells (BCs, blue) to retinal ganglion cells (RGCs, gray), the spiking output neurons of the retina. Horizontal cells and amacrine cells (green) provide lateral inhibitory connectivity in two synaptic layers. **(D)** Similarly, invertebrate R1–R6 PRs connect via lamina neurons (blue) to transmedullary neurons (TM; gray), and inhibitory connections (green) provide lateral feedback in two layers. In both vertebrates and invertebrates, PRs usually use a predominately graded mode of signal encoding, although there are a few exceptions. Secondary neurons in the sensory periphery can use a combination of spiking and graded modes of transmission. Projection neurons are all spiking neurons in the case of vertebrates (i.e., RGCs, but can use different graded and spiking modes of transmission in invertebrates (TMs).

full-blown APs [3]. Traditionally, BCs have been considered nonspiking neurons that drive transmitter release at their axon terminals through purely graded potentials [4,5]. However, recent evidence indicates that this picture is a simplification and that BCs in a range of species are also capable of generating spikes [6–10].

A similar overall organization exists in the compound eyes of insects, as exemplified by flies [11–14]. Here, graded PR signals from six PRs (R1–6) in each retinal module (ommatidium) converge to large monopolar cells (LMCs), which in turn provide input to transmedullary cells (TMs). Two other PRs (R7/R8) provide direct inputs to TMs. Depending on the type of neuron, both LMC and TM neurons generate a mixture of graded and spiking signals (e.g., [15,16]). TMs provide input to a wide range of visual interneurons in the lobula and lobula plate complex, which, again depending on the type of neuron, generate graded, mixed, or spiking visual responses [12,13]. Similarly, in the accessory visual system (ocelli), graded PR signals are transmitted to L-neurons, which can generate spikes in a manner similar to LMCs in the compound eye (e.g., [17]). As in the vertebrate retina, synaptic transmission in the compound eye is modified by inhibitory inputs

at all synaptic stages, most notably at the PR–LMC synapses [18]. Therefore, the propensity to generate graded and spiking responses in early visual neurons of both vertebrates and invertebrates is highly diverse, with various parallel pathways using different forms of A–D conversion at different processing stages (Figure 1).

How are analog and digital signals transmitted from one neuron to another? Intriguingly, the first sensory synapses transmitting information about light and sound are set apart from ‘conventional’ synapses by an unusual organelle, the ribbon, which aggregates vesicles close to the active zone (Figure 2). At conventional synapses, an AP lasting a few milliseconds triggers a transient burst of vesicle fusion. Ribbon synapses share many fundamental properties with conventional synapses and can also release vesicles in short, fast bursts. However, they also support a continuous mode of transmitter release, the rate of which varies continuously with graded changes in membrane potential. In vertebrates, ribbons exist in PRs and bipolar cells of the retina, and in mechanosensitive hair cells of cochlea and vestibular organs of balance, as well as in the lateral line of fish (reviewed in [19–23]). Notably, spikes and resonances have also been reported in hair cells (Box 1). Many insects have comparable

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