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Review Paper

Mathematical analysis and modeling of motion direction selectivity in the retina

Q1 María-José Escobar [a], Danilo Pezo [b], Patricio Orio [b,c,*]

[a] Universidad Técnica Federico Santa María, Department of Electronics Engineering, Avda España 1680, Valparaíso, Chile
[b] Centro Interdisciplinario de Neurociencia de Valparaíso, Universidad de Valparaíso, Avda Gran Bretaña 1111, Valparaíso, Chile
[c] Facultad de Ciencias, Universidad de Valparaíso, Avda Gran Bretaña 1111, Valparaíso, Chile

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ABSTRACT

Motion detection is one of the most important and primitive computations performed by our visual system. Specifically in the retina, ganglion cells producing motion direction-selective responses have been addressed by different disciplines, such as mathematics, neurophysiology and computational modeling, since the beginnings of vision science. Although a number of studies have analyzed theoretical and mathematical considerations for such responses, a clear picture of the underlying cellular mechanisms is only recently emerging. In general, motion direction selectivity is based on a non-linear asymmetric computation inside a receptive field differentiating cell responses between *preferred* and *null* direction stimuli. To what extent can biological findings match these considerations? In this review, we outline theoretical and mathematical studies of motion direction selectivity, aiming to map the properties of the models onto the neural circuitry and synaptic connectivity found in the retina. Additionally, we review several compartmental models that have tried to fill this gap. Finally, we discuss the remaining challenges that computational models will have to tackle in order to fully understand the retinal motion direction-selective circuitry.

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[*] Corresponding author at: Centro Interdisciplinario de Neurociencia de Valparaíso, Universidad de Valparaíso, Avda Gran Bretaña 1111, Valparaíso, Chile. Tel.: Q2 +56 322995538.
E-mail address: patricio.orio@uv.cl (P. Orio).

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1. Introduction

Motion detection is one of the most important and primitive computations performed by our visual system. In fact, the production of signals in the absence of movement is a property that is present only in most recent species in evolution. Motion is computed by our visual system at very early stages, such as, the retina, the LGN and the primary visual cortex (V1). Specifically in the retina, in the early 1960s Barlow and Levick (1965) reported a very specialized type of retinal ganglion cell in rabbits that does not only detect motion, but also, motion direction. The activity of this special type of ganglion cell, known as Direction Selective Retinal Ganglion Cell (DSRGC), is related to a specialized circuitry involving the integrated activity of bipolar and starburst amacrine cells (SACs). In the last 10 years, this circuitry has been deeply studied and characterized as can be seen in several recent reviews (Demb, 2007; Borst and Euler, 2011; Euler and Hausselt, 2012; Vaney et al., 2012). At least two types of DSRGCs are simultaneously present in the retina, with different motion detection properties and projecting to different places of the central nervous system (Berson, 2008; Kanjhan and Sivyer, 2010; Wei and Feller, 2011). The cells of the first subtype respond both to ON and OFF stimuli moving over a broad range of speeds, and are selective to one of the four different cardinal directions of motion (On–Off DSRGCs) (Barlow and Levick, 1965; Oyster, 1968). A second subtype of cells responds only to ON stimuli (On DSRGCs) and it is selective to three different motion directions aligned with the vestibular axes. In addition, On DSRGCs have larger receptive fields than On–Off DSRGCs, thus allowing them to respond to slow velocities (Barlow and Levick, 1965; Oyster, 1968). On–Off DSRGCs, referred to hereafter as DSRGCs, are the most common type and the models proposed to understand their motion direction mechanisms will be reviewed in this article. In doing so, we will try to link the existing mathematical models of motion detection to the known biological mechanisms and to the proposed biophysical models of the underlying circuitry.

Several approaches have been proposed to model motion detection and, particularly, selectivity to motion direction. Most of the models are based on detector units able to distinguish between *preferred* and *null* motion directions. In particular, efforts have been made to map motion detection properties to the retina motion detectors (e.g. Poggio and Reichardt, 1973; Torre and Poggio, 1978; Hildreth and Koch, 1987; Borst, 2007), but besides the work of Borst (2007), the link between the mathematical properties of motion detectors and the behavior of On–Off DSRGCs has not been studied in depth.

Biophysically inspired models, attempting to reproduce the motion computation performed by SACs and DSRGCs in the retina have also been proposed and they have been briefly covered by recent reviews (Borst and Euler, 2011; Euler and Hausselt, 2012). In this article, we address these types of models more deeply, making the links with the general mathematical models of motion detectors.

In an attempt to unify different worlds under a common scope and defining a common nomenclature, the most common theoretical motion detectors will be reviewed: Reichardt and Gradient (Section 2), after which, a counterpoint will be made with the existing evidence of motion computation mechanisms in the mammalian retina (Section 3). Afterwards, we will review compartmental models (Section 4), and outline for future challenges for computational models towards answering unsolved questions related to the motion direction circuitry in the retina (Section 5). Finally, Appendix A shows a mathematical analysis of the theoretical motion detectors described in Section 2, which complements previous numerical and analytic results shown in the literature.

2. The mathematical basis of motion detection and direction selectivity

2.1. Theoretical models

Motion detection models have been proposed since the very beginnings of vision science and vastly developed as proof of concept in order to better understand the mechanisms underlying this phenomenon. There are motion detection models for different levels and spatial scales, and these computational models replicate elements, interactions and functionality for each level. Regardless of the details of the model, every directionally selective motion detector must accomplish the following three requirements (Borst and Egelhaaf, 1989):

- *Spatial asymmetry:* Accounts for the necessary differences that the system must have in order to show preferred and null directions.
- *Two inputs and a time delay between the inputs:* A single input would only be able to detect the presence of the stimulus and not its direction, and at least two inputs are needed to discriminate between preferred and null motion directions. A time delay is necessary to allow the moving stimulus to interact with the motion detector, because the spatially separated inputs would be excited at different times.
- *Non-linear interactions:* In a motion detector, direction selectivity implies statistical differences in the time-average (or time-integral) of the $y(t)$ output in the preferred direction with respect to the null direction. If the interaction between inputs $z_1(t)$ and $z_2(t)$ is linear (such as $y(t) = az_1(t) + bz_2(t)$), the time-average of the output would be equal to a linear combination of the time-average of the inputs. As the time average lacks any temporal information, the time-average of $y(t)$ would be the same regardless of the temporal relationship between the inputs. Hence, the interaction between inputs $z_1(t)$ and $z_2(t)$ must be non-linear.

In the literature we can distinguish two types of basic (theoretical) motion detector models: Correlation detectors (Hassenstein and Reichardt, 1956; Poggio and Reichardt, 1973) and Gradient detectors (Fennema and Thompson, 1979). A brief account of these two models will be offered below.

The *Correlation detector* shown in Fig. 1(a) was originally proposed by (Reichardt, 1957), and hence it is also known as the Reichardt Detector. It consists of two mirror-symmetric subunits, each with a time delay (Δt) (that can be represented by a low pass filter

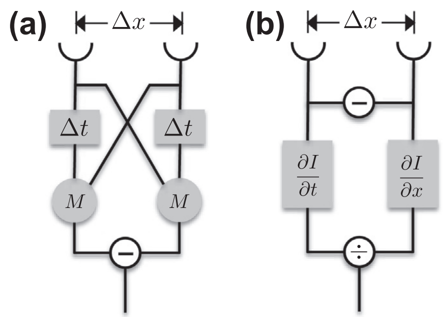

Fig. 1. Two main families of motion detection models. (a) In the Correlation detector, a subtraction operation between delayed and multiplied signals accounts for motion direction selectivity: motion in one direction produces a positive depolarizing output, and in the opposite direction the output is negative producing a hyperpolarizing effect. (b) The Gradient detector builds an estimation of the velocity through temporal and spatial changes of brightness.

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