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Construction and evaluation of an integrated dynamical model of visual motion perception

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ABSTRACT

Although numerous models describe the individual neural mechanisms that may be involved in the perception of visual motion, few of them have been constructed to take arbitrary stimuli and map them to a motion percept. Here, we propose an integrated dynamical motion model (IDM), which is sufficiently general to handle diverse moving stimuli, yet sufficiently precise to account for a wide-ranging set of empirical observations made on a family of random dot kinematograms. In particular, we constructed models of the cortical areas involved in motion detection, motion integration and perceptual decision. We analyzed their parameters through dynamical simulations and numerical continuation to constrain their proper ranges. Then, empirical data from a family of random dot kinematograms experiments with systematically varying direction distribution, presentation duration and stimulus size, were used to evaluate our model and estimate corresponding model parameters. The resulting model provides an excellent account of a demanding set of parametrically varied behavioral effects on motion perception, providing both quantitative and qualitative elements of evaluation.

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1. Introduction

Although our understanding of the underlying neural mechanisms of motion perception is incomplete, a range of motion processing models have been proposed to account for various properties of visual motion perception. Among those models, perceptual models provide a high-level characterization of stimuli and perception, and neural models suggest biologically plausible mechanisms to process motion information. Of course, perceptual models often propose possible neural mechanisms, and neural model properties often show direct connections to known perceptual phenomena. Yet, the links between the two levels of analysis can be sketchy: Sometimes, the connections between the neural components are not well understood; sometimes studying the resulting complex systems requires the application of a wide range of analytic procedures and significant computational power.

With increasing precision of experimental measurements and computational power for simulations, it has become possible to design and implement visual motion models encompassing both neurophysiology and psychophysics, further explicating the links between perception and its neural substrate. In doing so, a successful visual motion processing model will incorporate and implement various neural components associated with different neural populations at multiple levels of visual motion processing, including components for motion detection, motion integration, perception, and decision.

In the literature, neural motion models typically consider two-stages of motion processing where a local motion detector typifies processing in primate cortical area V1 (Adelson & Bergen, 1985; van Santen & Sperling, 1984) and feeds motion information to a large scale integrator associated with area MT (Heeger, Simoncelli, & Movshon, 1996; Rust, Mante, Simoncelli, & Movshon, 2006; Simoncelli & Heeger, 1998)

There have been a number of attempts to extend the traditional two-stage model. The models of Chey, Grossberg, and Mingolla (1997, 1998) include variants to account for motion detection and motion integration, yet provide only qualitative comparison of model predictions to experimental results. Similar models have been proposed to investigate the role of feedback between cortical areas V1 and MT (Bayerl & Neumann, 2004), to include form–motion interactions (Bayerl & Neumann, 2007; Beck & Neumann, 2010; Berzhanskaya, Grossberg, & Mingolla, 2007), to further study the dynamics of motion integration

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(Tlapale, Masson, & Kornprobst, 2010), or to consider rotations and expansions (Raudies, Mingolla, & Neumann, 2011). Those models extend the traditional two-stage motion models (Heeger et al., 1996; Rust et al., 2006; Simoncelli & Heeger, 1998), effectively solving the motion aperture problem through non-linear normalization, and include various initial motion detection stages based on specific neural computations (Chey et al., 1997, 1998), phenomenological models (Bayerl & Neumann, 2004), or motion energy models (Tlapale et al., 2010).

Bayesian models have been used to model motion perception at a higher level (Weiss & Adelson, 1998; Weiss, Simoncelli, & Adelson, 2002) or eye movements (Bogadhi, Montagnini, Mamassian, Perrinet, & Masson, 2011; Montagnini, Mamassian, Perrinet, Castet, & Masson, 2007). Typically those models assume probabilistic inputs and outputs, with various levels of abstraction, such as segregation between 1D and 2D components (Montagnini et al., 2007), and define some quantitative value to be maximized. Although general neural implementation strategies for Bayesian mechanisms have been proposed (Rao, 2004), as is the case for other optimization methods such as variational approaches (Viéville, Chemla, & Kornprobst, 2007), the link to the effective neural computations is often not well specified. Indeed the focus and power of those approaches lie in the high level description of the task performed by the neural system, with respect to its a priori knowledge.

Physiologists have applied standard models of decision-making to random dot motion and other stimuli. Perceptual decisions in two-alternative forced choice are represented in drift diffusion models in which positive or negative evidence accumulate until a threshold is reached (Ratcliff, 1978; Stone, 1960). More recently, Wang (2002) constructed a spiking neural network accounting for a range of perceptual decision making experiments in random dot motion, and later provided a neural field approximation of their model (Wong, Huk, Shadlen, & Wang, 2007; Wong & Wang, 2006), while Machens, Romo, and Brody (2005) proposed a model for two interval forced choice decision paradigms. To make computational and mathematical analysis tractable, most of those approaches assume static or minimum representations where the input typically represents two subpopulations of MT neurons corresponding to the two choices in a forced choice paradigm, with an average activity given by a linear function of the motion coherence level in the stimulus (Mazurek, Roitman, Ditterich, & Shadlen, 2003; Wong et al., 2007; Wong & Wang, 2006).

Finally, the influence of internal and external noise on perception is largely ignored in multi-scale models. Yet, noise is an important component of both the stimuli and the processing at every level of the visual system. In the motion domain, the classic random dot kinematograms are defined by the large amount of (external) noise they contain. Manipulating stimulus noise is also a particularly useful tool to analyze a system, allowing researchers to distinguish between several types of internal noise (Lu & Dosher, 1999, 2008) and to investigate the influence of top-down signals (Lu & Dosher, 1998).

We propose an integrated dynamical motion (IDM) model of motion perception that incorporates biologically plausible motion detection and motion integration mechanisms, as well as a decision mechanism to account for reaction times in perceiving motion from random dot kinematograms. Our model includes temporal dynamics that allow us to consider the systematic stimulus variations and corresponding empirical results such as those described in Watamaniuk and Sekuler (1992) and Watamaniuk, Sekuler, and Williams (1989). Such parametric variations, including systematic changes of random dot distribution, presentation duration and stimulus size, remain uncommon in research on motion perception, but provide an empirically grounded test bed for models of motion perception.

In Section 2 we detail the design of the multi-scale model of motion perception based on the known architecture of the visual system. We also make use of dynamical simulations and numerical continuations to identify stable regions of the parameter space for model implementation. In Section 3 we focus on modeling the set of random dot experiments in Watamaniuk and Sekuler (1992) and Watamaniuk et al. (1989). We show that the model is able to account for the experimental data and specify the corresponding parameters. In Section 4 we discuss the biological plausibility of the model, compare it to alternative approaches, and conclude with future extensions of the framework.

2. Model

To reproduce, explain and predict motion perception and perceptual decisions from specific motion stimuli, we devised a detailed integrated dynamical motion (IDM) model of visual motion perception. The model is grounded in the current anatomical and electrophysiological knowledge of the human and primate visual system. As such it follows the typical multi-stage view of motion integration, where a first stage detects motion and is linked to the activity of V1 or MT component cells (Section 2.1), while a second stage integrates the activity to extract global motion and is linked to the activity of MT pattern cells (Section 2.2). The model is able to reproduce a variety of MT neural responses, and explain the corresponding motion percepts with additional decision mechanisms linked to neural processing in area LIP (Section 2.3). The interactions between the three layers are represented in Fig. 1.

2.1. Motion detection

We follow a standard approach to define directional V1 cells by combining the responses of two non-directional V1 subpopulations. Formally, we start by representing stimuli as varying luminance values, noted $I(t, x, y) \in \mathbb{R}$ where t, x, and y, are the temporal and visual field positions. The difference between this approach to direction selectivity in V1 and prior approaches (Adelson & Bergen, 1985; Escobar, Masson, Viéville, & Kornprobst, 2009) is the use of temporally monophasic filters matching primate cell recordings (De Valois & Cottaris, 1998; De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000), in addition to the temporally biphasic filters.

The response of directional cells tuned to direction θ is defined by

$$D(t, x, y, \theta) = (M_\theta + B), \overset{t,x,y}{*}, I(t, x, y), \tag{1}$$

where $\overset{t,x,y}{*}$ denotes the spatiotemporal convolution operator, M_θ, is the kernel of temporally monophasic, spatially odd neurons (the *lower left* component in Figs. 1 and 2), and B is the kernel of temporally biphasic, spatially even neurons (the *lower right* component in the same figures). The kernel of monophasic neurons is defined as

$$\begin{aligned} M(t, x, y) = {} & \Gamma_{n_M, \tau_M}(G_{\sigma_M}(x - a\cos\theta, y - a\sin\theta) \\ & - G_{\sigma_M}(x + a\cos\theta, y + a\sin\theta)), \end{aligned} \tag{2}$$

where $\Gamma_{n,\tau}$ and G_σ are temporal and spatial localization functions respectively, and defined as

$$\Gamma_{n,\tau}(t) = (nt)^n \frac{\exp(-nt/\tau)}{(n-1)!\,\tau^{n+1}}, \tag{3}$$

which is a Gamma function (de Vries & Principe, 1991), and

$$G_\sigma(x, y) = \frac{1}{2\pi\sigma^2} \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right), \tag{4}$$

which is a Gaussian function with standard deviation (spread) σ.

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