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Review

# The behavioral receptive field underlying motion integration for primate tracking eye movements

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ABSTRACT

Short-latency ocular following are reflexive, tracking eye movements that are observed in human and non-human primates in response to a sudden and brief translation of the image. Initial, open-loop part of the eye acceleration reflects many of the properties attributed to low-level motion processing. We review a very large set of behavioral data demonstrating several key properties of motion detection and integration stages and their dynamics. We propose that these properties can be modeled as a behavioral receptive field exhibiting linear and nonlinear mechanisms responsible for context-dependent spatial integration and gain control. Functional models similar to that used for describing neuronal properties of receptive fields can then be applied successfully.



**Contents**



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## 1. Introduction: object motion computation for gaze stabilization

Visual motion is critical for the guidance of slow eye movements that help visual perception by stabilizing the images onto the retina. However, in a crowded and constantly changing visual environment, stabilizing the whole retinal image is largely inappropriate. Our visual system must parse these images into separate objects, select the one of interest and accurately measure its motion in order to smoothly rotate the eyes at the appropriate speed and direction. Primates are equipped with extremely fast and accurate oculomotor behaviours. Since the mid 20th century, the primate oculomotor system is probably one of the best known of the sensorimotor systems (see Leigh and Zee, 2006). Many review articles are available from the literature. For instance, Keller and Heinen (1991) and Ilg (1997) gave exhaustive reviews of the classification of the different types of smooth eye movements and their neural substrates. Krauzlis and Stone (1999) documented the behavioral evidences that smooth and saccadic eye movements are closely linked together. More recently, Krauzlis (2004) has recasted the neural framework of smooth pursuit eye movements and its links with the saccadic systems. However, very few review articles have been dedicated to the more specific topic of visual motion processing in the context of sensorimotor transformation. Miles and colleagues (e.g. Kawano, 1999; Miles, 1993, 1997, 1998; Miles et al., 2004) have published several reviews that summarizes their pioneering work on optic flow processing and reflexive slow eye movements. Still, a review article focusing the consequences of early visual motion computation is missing.

This review takes a different viewpoint about eye movement control. We are interested in the fundamental visual mechanisms underlying this sensori-to-motor transformation. As pointed out by Miles (1993) most models of smooth eye movements collapse this complex processing into a single box that measures retinal target velocity, or higher derivatives needed to feed the motor control mechanisms. Thus, understanding the visual motion processing stage of visuomotor behaviors is a major challenge in systems neuroscience. Lisberger et al. (1987) offered a classical introduction to this fascinating question. In a more recent review, he summarizes the results obtained from his group supporting the idea that voluntary pursuit is initiated based upon a rapid linear read-out of area MT neurons (Lisberger, 2010). Thus, it appears after two decades of intensive work that many of the dynamical aspects of eye movements are in fact constrained by the neural solutions of visual motion processing (see also Masson, 2004; Ilg, 2008; Masson and Ilg, 2010). In this perspective, tracking eye movements offer a miniature model of perception–action coupling.

Herein, our objective is to provide an updated view of the complex front-end processing that computes object motion for visuo-motor control. Our review documents the experimental work conducted by several groups to elucidate the properties of ocular following responses in both human and non-human primates. Thus, we will restrict our scope to the initial, open-loop part of the reflexive responses. In this well-defined framework, it becomes possible to relate neural and behavioral dynamics with a very high level of details (Lisberger et al., 1987; Miles, 1997; Kawano, 1999). Each aspect of the motor responses can be mapped with a specific aspect of visual information processing. These linear and non-linear mechanisms can be summarized within a concept called the *behavioral receptive field* that concisely describes how information is integrated within populations of cortical neurons in order to extract the relevant signals (i.e. speed and direction) about a single object motion (Barthélemy et al., 2006). This idea is reminiscent of the earlier notion of perceptive fields but offer a more precise framework, in particular regarding the temporal dynamics of information processing. Such behavioral receptive field incorporates many of the fundamental aspects of sensory information processing such as spatial and temporal filtering, spatial summation, nonlinear gain control and multiple feature integration. Each of these aspects can be fitted with mathematical tools already used at both population and neuronal levels to describe classical and non-classical receptive fields.

Such behavioral receptive field can be seen as a read-out of low-level cortical computations done through the recurrent connectivity between areas V1 and MT/MST. These first 100 ms of ocular following offers a minimalist, but very efficient window onto these mechanisms. Whenever it is possible, we will compare the tuning properties and their temporal dynamics of the behavior with the neuronal mechanisms observed at each of these cortical stages. Although the scope of this review might sounds a bit too much focused on a particular type of eye movements, we advocate herein the usefulness of such a delicate approach to elucidate the detailed temporal architecture of the brain.

The review is organized as follows. We will first recast ocular following as one example of short-latency, reflexive smooth movements of the eyes that have been identified in both human and non-human primates. From neurophysiological studies conducted in macaque monkeys, we will present the underlying cascade of cortical and sub-cortical steps driving response onset, aiming at extracting the key stages that are essential to understand the behavioral results that will be presented subsequently. We will then define the behavioral receptive field, in the perspective of an older theoretical concept from visual perception, the perceptive field. Both concepts are defined from behavioral (i.e. motor versus perceptual) phenomenology, but we propose that the ocular following approach allows us to better constrain the core idea and therefore will open the door for realistic modeling. Indeed, we will review behavioral properties of ocular following when tackling the classical computational stages of visual motion processing: (i) what are the detection mechanisms, (ii) how local motion in pooled to extract direction and speed information and (iii) how are these mechanisms dependent upon visual context? At each stage we highlight the key results that will be then used to define the mathematical description of its input–output transfer function. We will then close this review by highlighting some open questions.

## 2. Ocular following: reflexive tracking in human and non-human primates

Since the pioneering work of Dodge (1903), several sub-types of visually driven smooth eye movements have been defined. This classical taxonomy distinguishes between reflexive optokinetic eye movements that are driven by large field visual motion to form the slow phases of OKN, and voluntary smooth pursuit eye movements that are elicited by local visual motion. They both have short latency, mostly around or below 100 ms in primates. Eye speed