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Critical revision of the neurophysiology of tracking eye movements

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► **To cite this version:**

Laurent Goffart. Critical revision of the neurophysiology of tracking eye movements. GDR conference NeuralNet 2018, Dec 2018, Paris, France. hal-03654901

HAL Id: hal-03654901

<https://hal.science/hal-03654901v1>

Submitted on 29 Apr 2022

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1. When a subject looks at a visual target in the physical world, her/his eyes rotate in such way that the target image is first brought within the fovea and then maintained for a time interval which is more or less long (unstable equilibrium).

For the purpose of simplicity, most neurophysiological studies used targets whose shape is bounded and does not change over time. Thus the targets, like the eyeballs, are rigid objects and their spatial attributes can be quantified by simple numerical values expressed within a convenient and common (mathematical) reference frame. A saccade is the very rapid eye movement made when gaze is shifted toward another target.

In response to a moving target, two types of eye movement: a saccade (interceptive, catch-up) and a slow eye movement (pursuit).

2. Attributing numerical values to the directions of gaze and target or the velocities of their movement inevitably leads to mismatches between them. Numerical differences do not imply corresponding mismatches within the brain activity.

Because of the divergence of anatomical connections, any stimulus leads to the excitation of a large number of neurons. Like visual neurons, visuomotor and motor neurons have an **extended response field**. This extent implies that any movement is associated with the excitation of a large set of neurons. Moreover, in most visual and visuomotor regions, neurons are laid out such that neighboring neurons respond to stimuli appearing in neighboring regions of the visual field, or fire a burst of action potentials during saccades toward neighboring locations in the physical world. Despite divergent anatomical connections, the **retinotopy** is preserved.

CONSEQUENCE : Neighboring objects, saccades toward their location, recruit populations which involve common cells. This functional overlap is overlooked when the difference between gaze and target directions (position error) or velocities (velocity error) are proposed to be commands driving the oculomotor system.

4. Attempts have been made to test whether the firing rate of neurons fits with the eye movement velocity. Yet, the velocity profile depends upon the sampling process. If the onset and rate of sampling were variable, the time course of identical saccades would show different profiles. When the time course of the neurons' firing rate differs from the time course of saccades, the notion of noise is introduced as a neural fact, **as if the brain processes ought to operate like our measuring instruments**, i.e., incrementally. Mapping the change of neuronal activity with the velocity of the movement of a rigid body (eyeball or object) supposes a one-to-one correspondence between the dynamics of multiple flows of neural activity (non-rigid) and one single time series. Supposing such a homeomorphism overlooks the fact that the brain activity corresponding to any situation (measured here and now) is not reducible to a point.

6. Diverse kinematical parameters (position, velocity and acceleration errors) have been considered as signals encoded in the distributed activity of neurons in the brain. Using statistical procedures fitting the relationship between a linear combination of these parameters and the neuron's firing rate over a short time interval, the activity of single neurons in various brain regions is sometimes interpreted as conveying kinematical functions, e.g.,

$$FR(t-\Delta) = a.pos(t) + b.vel(t) + c.acc(t) + d \quad \text{with } -100 \text{ ms} < \Delta < +100 \text{ ms}$$

pos = eye position ; *vel* = eye velocity ; *accel* = eye acceleration

Sun et al. Scientific Reports 2017 :

"In our present study, we found that both saccade- and SPEM-related responses of individual PCs could be predicted well by linear combinations of eye acceleration, velocity and position. The relative weights of the contributions that these kinematic parameters made depended on the type of eye movement"

8. The correlation between the spike discharge and kinematics might be saved by retrogradely tracking the origin and timing of action potentials that converge more or less synchronously onto the recorded neuron. However, this kind of analysis is complicated by the fact that afferent signals are transmitted through **axons of different lengths and conduction speeds**. The firing of a neuron is driven by action potentials emitted at different times by neurons located in different regions.

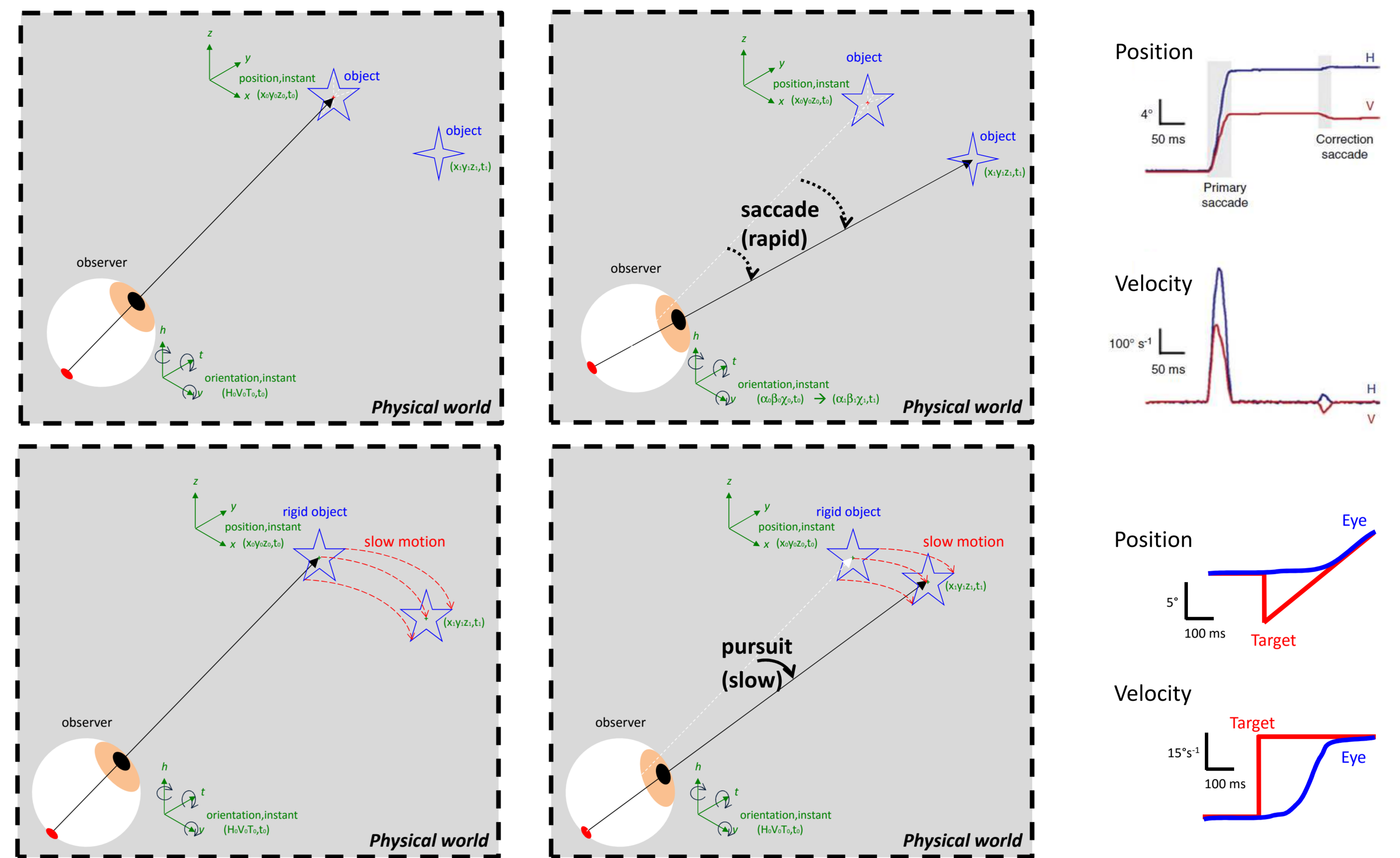
CONSEQUENCE : The time interval during which we estimate the instantaneous eye velocity is the outcome of action potentials delivered during a **different but also longer time interval**.

The temporal blurring is complicated by the fact that the activity does not remain bounded but spreads toward neighboring cells (Sparks et al. 1976; Anderson et al. 1998).

CONCLUSION : correlating the firing rate of central neurons with the velocity of any movement is a questionable procedure.

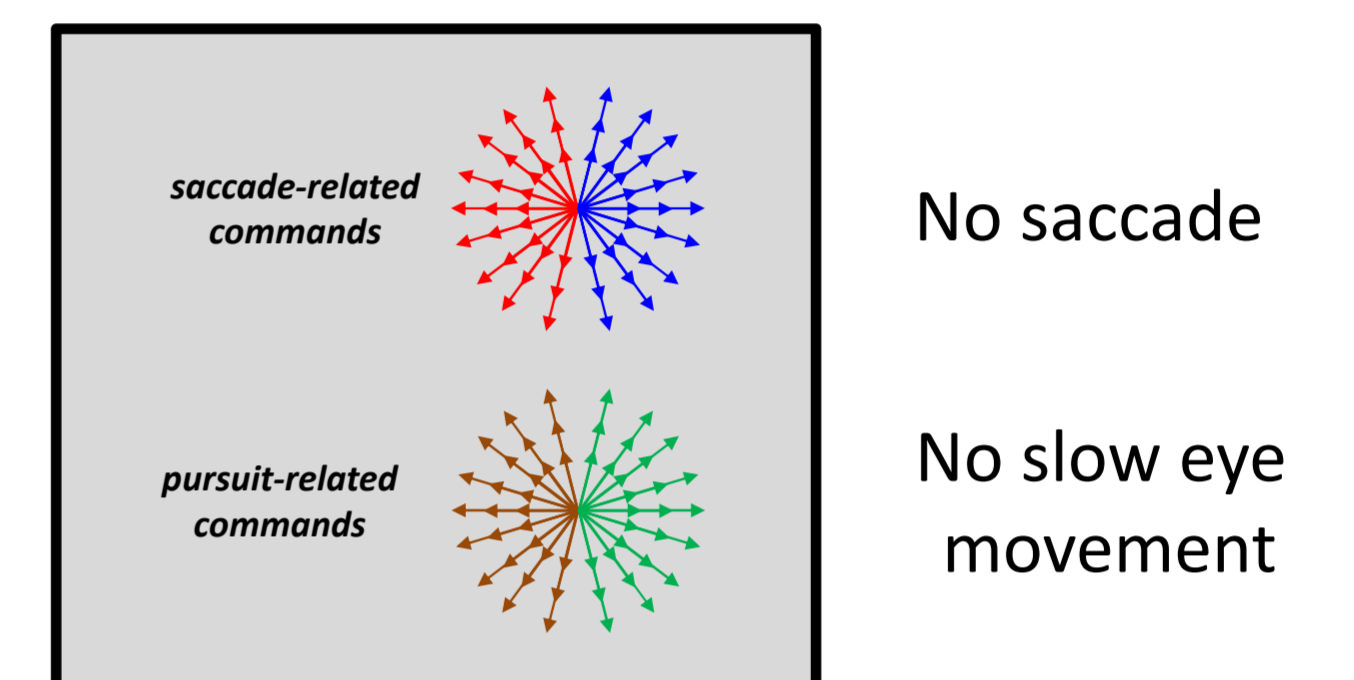
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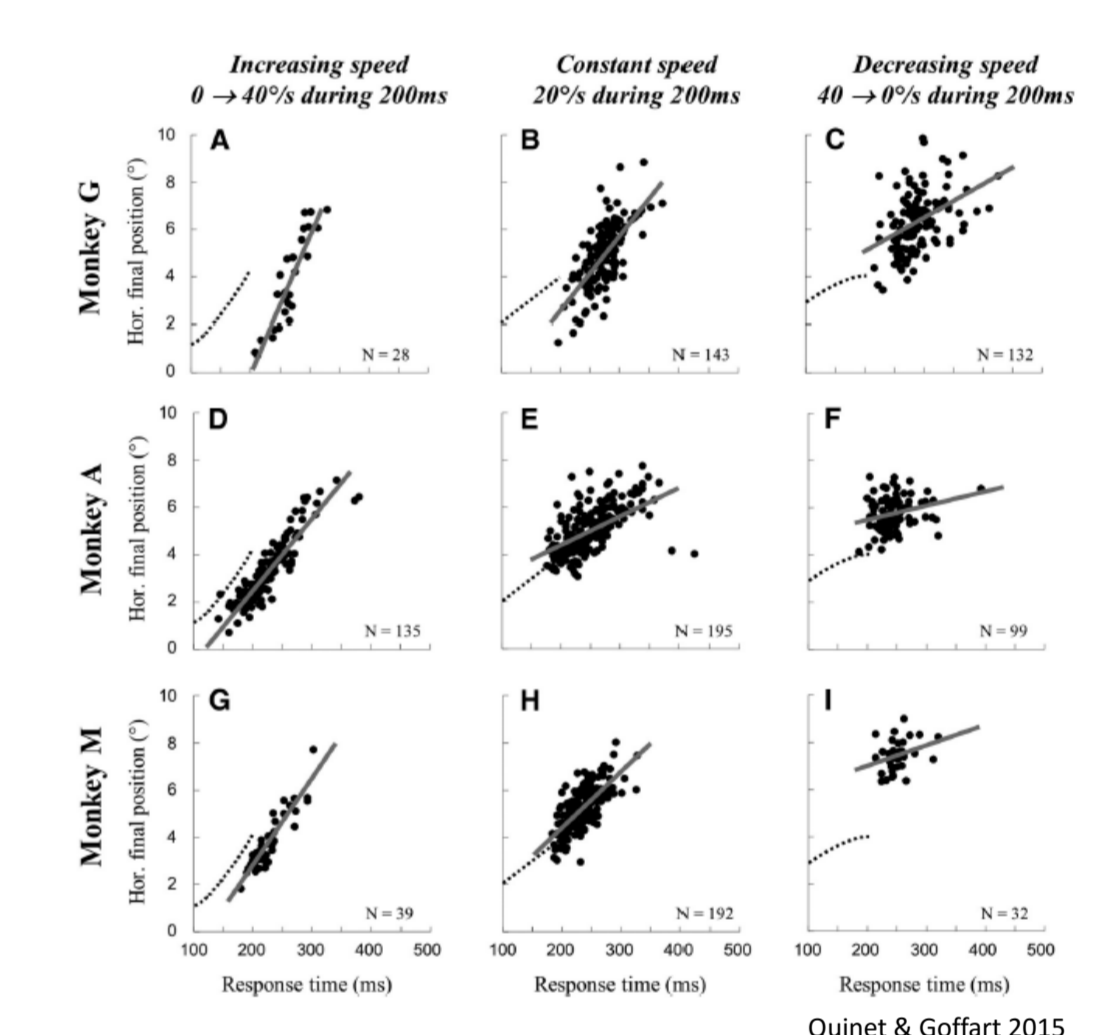
3. The overlap could very well participate in the triggering of movements insofar as a saccade may not be launched if the visuo-oculomotor system is within a mode where opposite commands **counter-balance** each other. Likewise, a slow eye movement may also involve a similar symmetry breaking (though involving a different chain of neurons). From this viewpoint, a movement is the **restoration** of an equilibrium of visuomotor activities while its triggering merely results from a **broken symmetry** (Goffart et al. 2018).

Behind absent measurable movement :
Equilibria of visuomotor activities



5. In addition to be spatiotemporally distributed in the brain, target-related activities do not change as fast as the measured coordinates of an object moving in the visual field. When we study eye movements pursuing a target which suddenly disappears, we find several instances where gaze keeps moving beyond the time of target disappearance (Mitrani & Dimitrov 1978). Likewise, saccades made in response to a transient moving target direct gaze toward locations where the target never went (Quinet & Goffart 2015). These examples of **persistence** illustrate the mass of activity hidden behind each measured position. See also the recordings of SC neurons (Goffart et al. 2017b).

Saccades toward a transient moving target



7. When we consider the discharge of motor neurons innervating the extraocular muscles, the correlation between the saccade kinematics and the train of action potentials can be interpreted relatively well because the action potentials cause the contraction of extraocular muscle fibers which in turn, yields the rotation of the eyeball.

When we consider now the firing of the premotor neurons which drive the motor neurons, the interpretation of the correlation is complicated by the fact that several inputs converge onto the motor neurons: from saccade-related burst neurons located in the ipsilateral paramedian reticular formation, from saccade-related burst neurons in the contralateral medullary reticular formation and from burst-tonic neurons located bilaterally in the left and right nuclei *prepositus hypoglossi* and medial vestibular nuclei (Scudder et al. 2002; Sparks 2002). The discharges of afferent groups do not exhibit identical time courses. The command is conveyed by neurons distributed across several nuclei; the correlation between their firing rate and saccade kinematics becomes weakened with more central neurons.

