

**Are kinematic parameters encoded
within the brain activity
while a gaze movement is being achieved
toward a visual target?**

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During the last decades, the laws of “classical” mechanics have been imagined to be internalized within the functioning of the brain of animals, as a result of their phylogenetic and ontogenetic adaptations to their own world (*Umwelt*).

In the framework of Newtonian mechanics, the motion is defined as coupled changes (ΔP and Δt) affecting a body within a homogeneous and inert receptacle (“space”), a medium which is neither altered by moving rigid bodies nor altering them. The chronometer and the pair of dividers are instruments that enable us to faithfully quantify the movement of an object.

Should we consider that a similar situation happens within the brain of an animal while it captures a moving object ?

How do we relate the motion of a rigid body (with its spatial and temporal coordinates) to the brain intrinsic events ? The latter consisting of non rigid activities propagating within a medium which is neither homogeneous, isotropic, inert nor permanent

Let's consider a spot of light in the visual field.

At the output of the optic nerve, the retinal excitation triggers a flow of activity exhibiting a kind of **arborescent explosion** (spatially distributed and temporally persistent). This explosion transforms into a kind of **compression** whose duration only matters. However, the parallelism of neuronal channels enables the corresponding “mobile” in the brain to be “**enlarged**” : an orienting movement can indeed be made by the eyes only or by a combined movement of the eyes and head (head movement related channels complement the oculomotor channels).

While the trajectory of a rigid body in the physical world can be described as a curve (with no thickness), its cerebral correlate is “spatially” and “temporally” different : it is diffusive and elastic.

Moreover, the cerebral medium is neither permanent nor inert ; it is plastic and changing. The ability to track a moving target (“here and now”), to synchronize the eye movement with the target motion is not spontaneous (“innate”) ; it requires a learning phase during which the cerebral functioning changes (augmentation of resources, change of transmission delays).

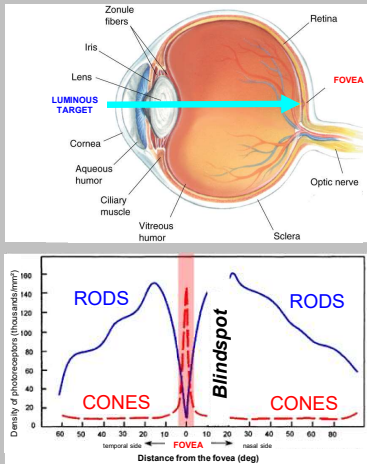
During the last decades, a confound has been made between kinematic quantifications and the underlying physiological processes that cause them.

Limitations of measurements and their associated theoretical notions led to imagine disputable options such as codings of space, time, duration, speed, acceleration ... in the brain

Kinematic parameters of gaze would be “encoded” within the neuronal activity. When they emit action potentials, the neurons would “speak” a language conveying notions of mechanics. Yet, any movement is merely one measurable product, one outcome of neuronal processes unfolding in the brain.

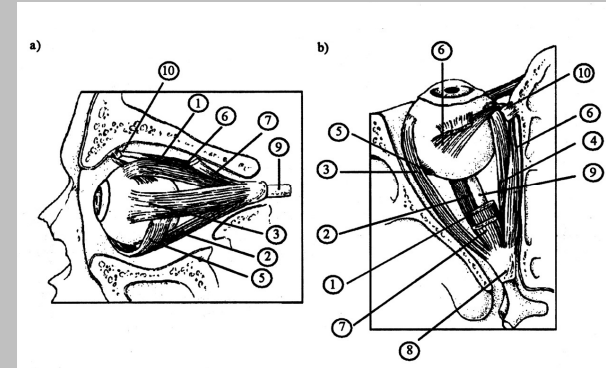
Another major concern is that, to the behavioral measurements, i.e., to the totally ordered set of numbers quantifying eye and head orientations correspond a partially ordered set of elements overlapping, spatially and temporally.

Looking at a visual target

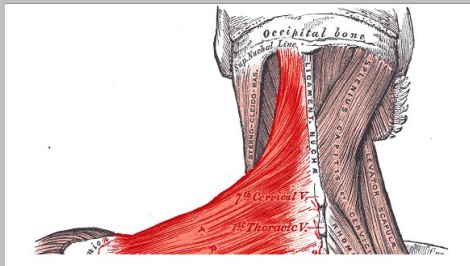


Non-homogeneous distribution of photoreceptors

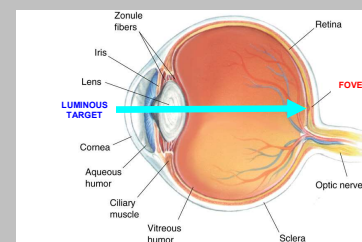
The projection of a target onto the fovea **requires** a proper contraction of extraocular muscles (gaze direction)



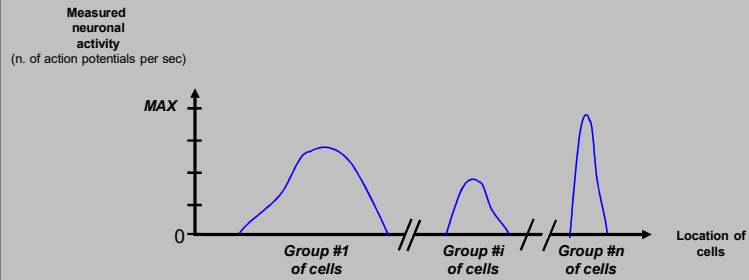
The projection of a target onto the fovea **also requires** a proper contraction of neck muscles (head direction)



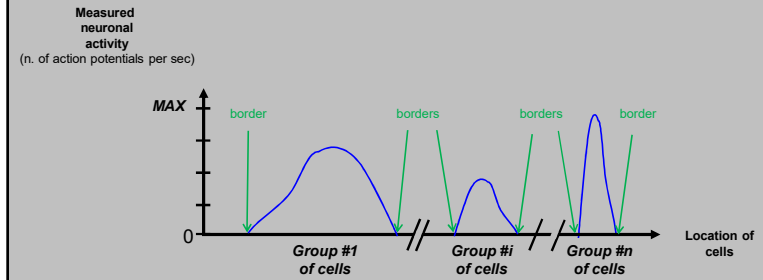
Looking at a visual target **IS** contracting multiple muscles



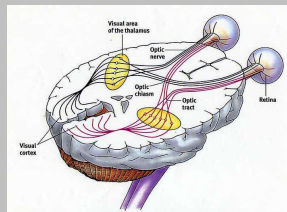
Multipolar distributed activity with gradients during a given task (*look at the object*) at a given instant



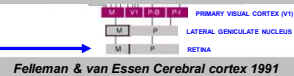
Multipolar distributed activity with gradients and flexible shape and borders



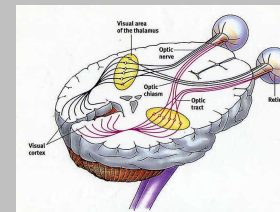
From the retina to the primary visual cortex,



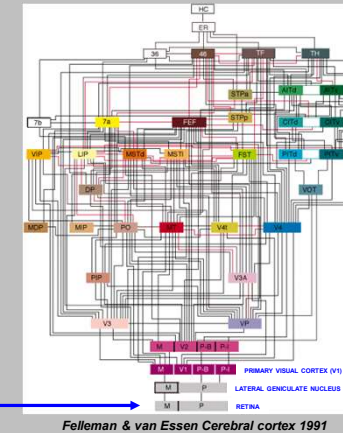
RETINA



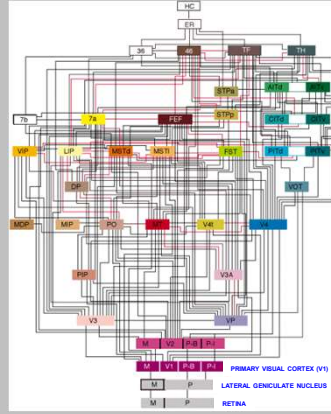
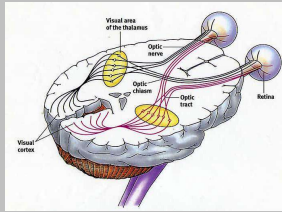
the activity spreads over multiple cortical regions



RETINA



The activity spreads also over multiple subcortical regions

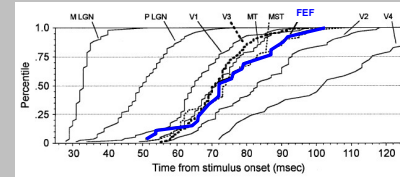


Felleman & van Essen Cerebral cortex 1991

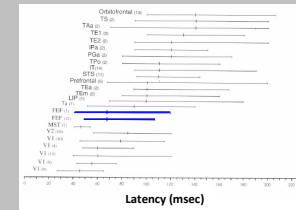


- Largely incomplete schema
- Pulvinar
 - Nucleus of Optic Tract
 - Superior Colliculus
 - etc ...

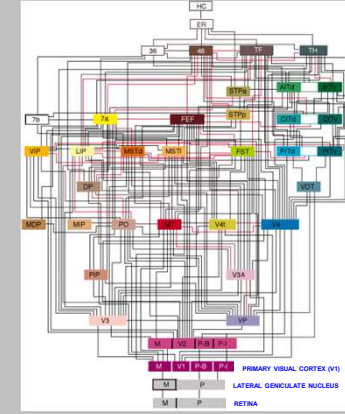
"Spatial" AND "temporal" spread of activity



Schmolesky et al. J Neurophysiol 1998

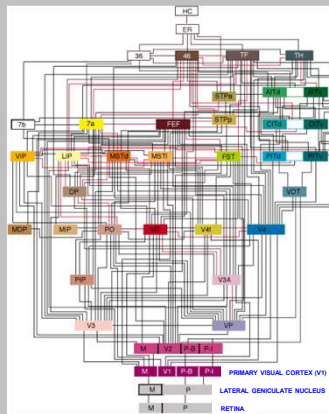


Nowak & Bullier Cerebral cortex: extrastriate cortex in primates 1997

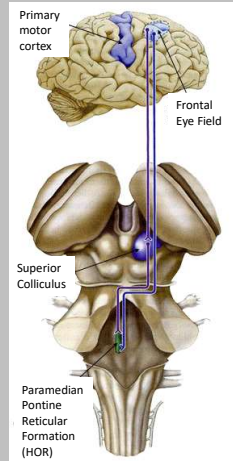


Felleman & van Essen Cerebral cortex 1991

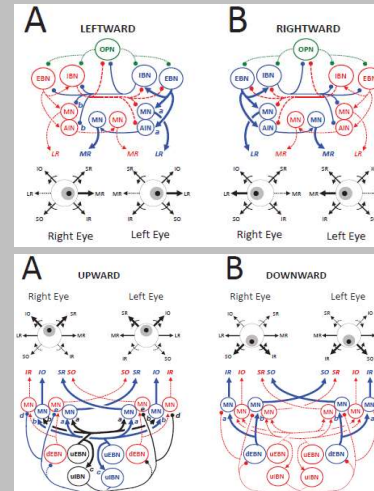
Convergence to premotor and motor centers



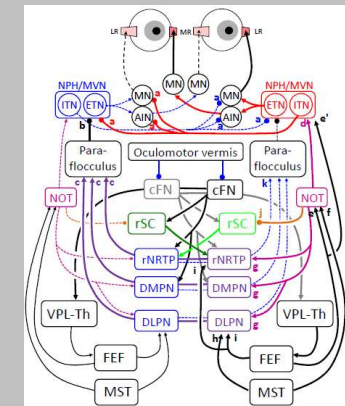
Felleman & van Essen Cerebral cortex 1991



Core neuronal networks



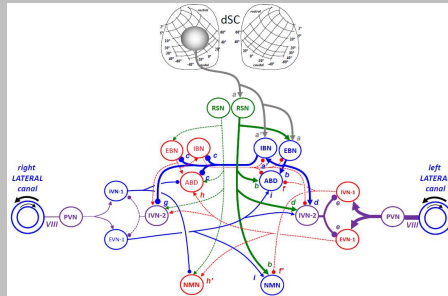
Pursuing a slowly moving target



Goffart, Quinet & Bourrelly Encyclopedia Human Brain submitted

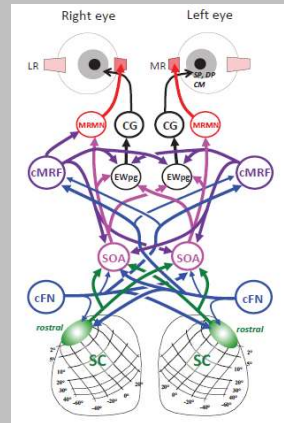
Core neuronal networks

Eyes and head orienting to the left



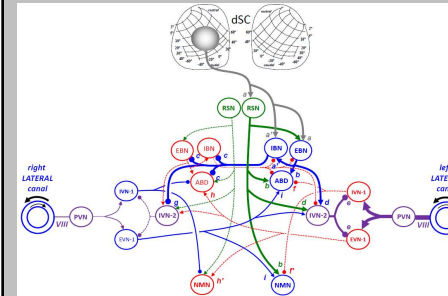
Goffart, Quinet & Bourrelly *Encyclopedia Human Brain* submitted

Looking at close versus far targets



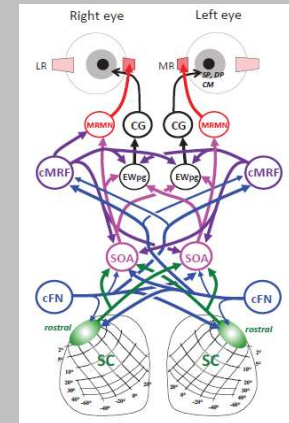
THIS KNOWLEDGE WOULD NOT HAVE BEEN POSSIBLE WITHOUT THE USE OF MONKEYS AND CATS

Eyes and head orienting to the left



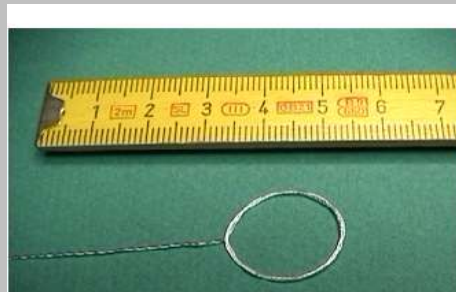
Goffart, Quinet & Bourrelly *Encyclopedia Human Brain* submitted

Looking at close versus far targets

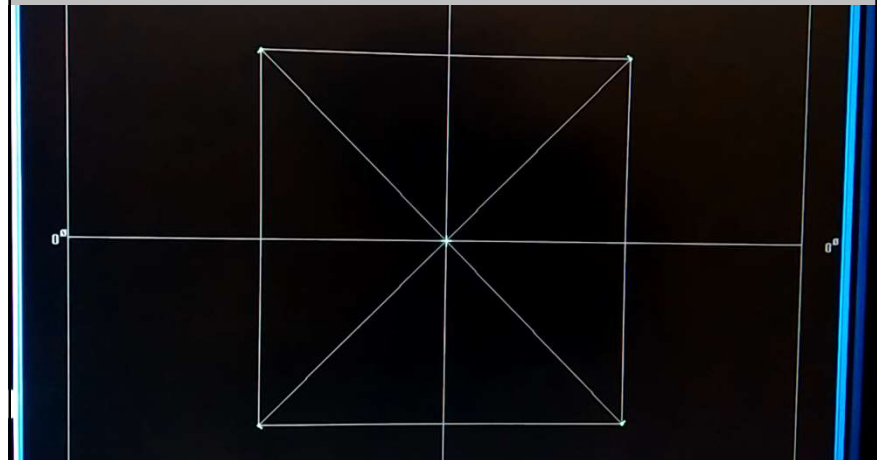


Recording of eye movements

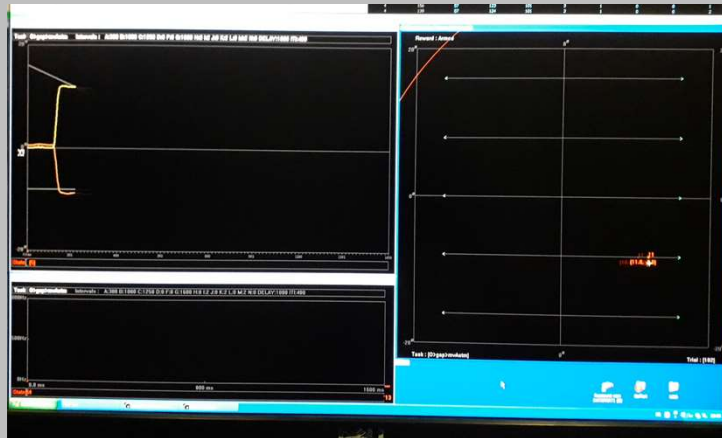
- Electro-magnetic induction
- Scleral coil
- 2 magnetic fields : H and V



Tracking eye movements in the trained monkey



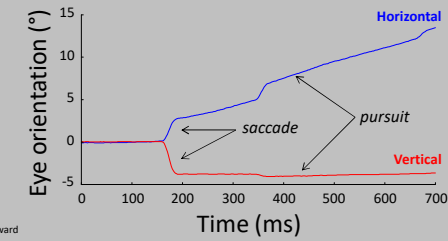
Tracking eye movements in the untrained monkey



Two types of eye movement in response to the motion of a visual target

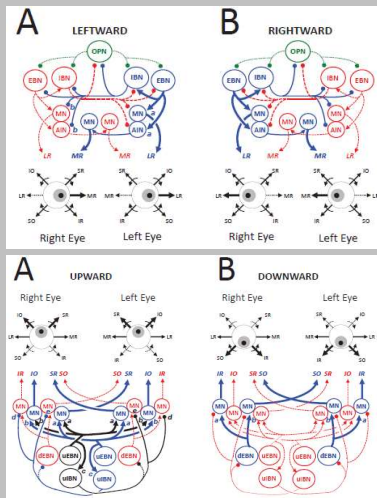
rapid : saccade
slow : pursuit

same muscles and motor nuclei BUT largely distinct central circuits

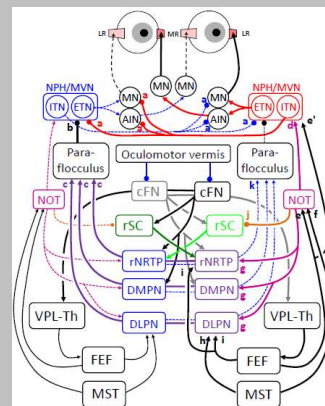


values > 0 : rightward / upward
value = 0 : straight ahead
values < 0 : leftward / downward

SACCADE NETWORK



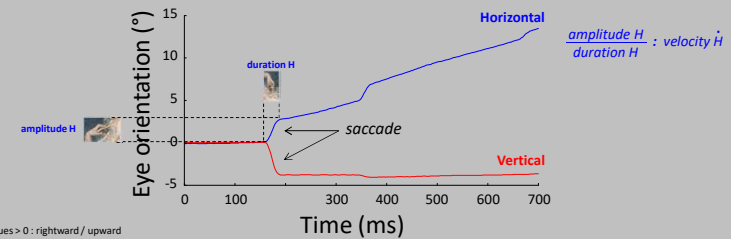
SLOW PURSUIT NETWORK (Horizontal)



Goffart, Quinet & Bourrelly *Encyclopedia Human Brain* submitted

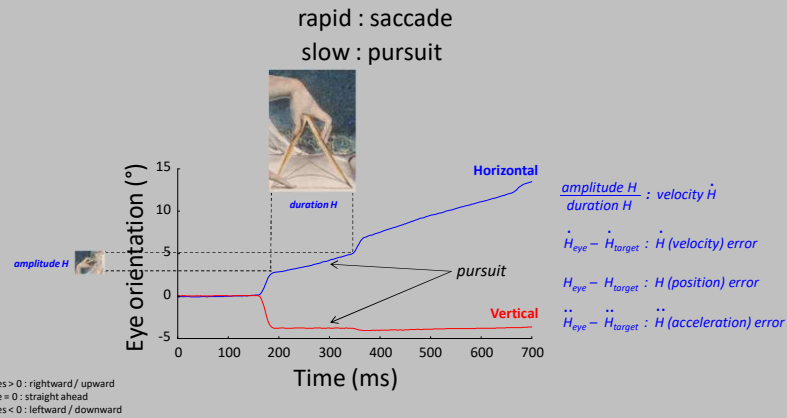
Two types of eye movement in response to the motion of a visual target

rapid : saccade

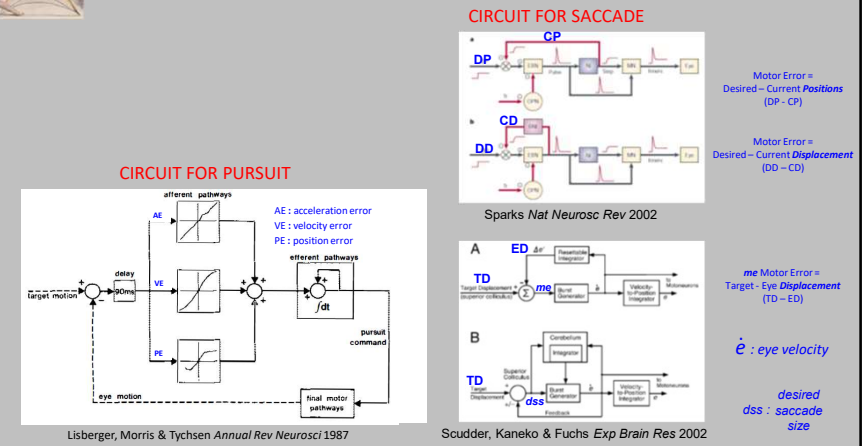


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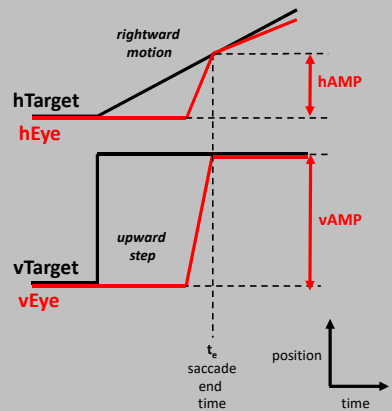
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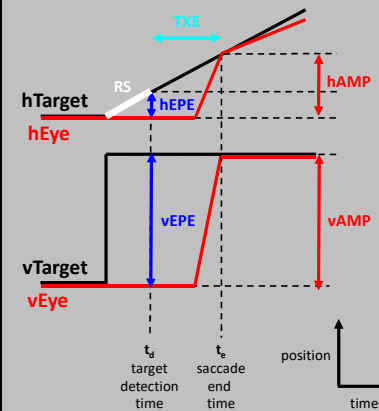
Dividers, physical quantities and arithmetic in the brain ?



From behavioral measurements to inferring putative neural processes



Dual-drive hypothesis



ASSUMPTIONS :

1. Snapshot of Eye Position Error (EPE)
2. Snapshot of Retinal Slip (RS)
3. Calculation of $T_{XE} = -\frac{EPE}{RS}$ (eye crossing time)

"eye crossing time," which is the time necessary for the eye to cross the target at constant eye velocity ($T_{XE} = -PE/RS$). For saccade trials, T_{XE} was evaluated on the basis of the retinal slip and position error 125 ms before saccade onset.

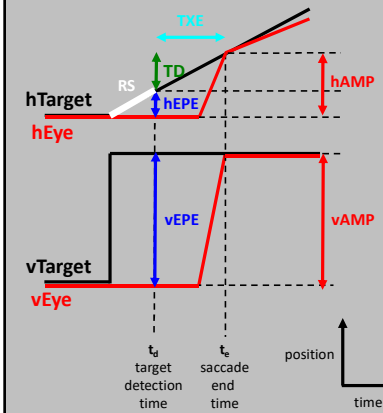
Predictive chronometric control in the brain ?

"Apparently, in cats as in humans, to determine an appropriate strategy, the saccadic system takes into account the **initial position and velocity of the target and the initial position of the eyes**. Based on these variables, **the system "predicts" the time remaining till the "collision" of the target with the line of sight.**" (Klam, Petit, Grantyn & Berthoz EBR 2001)

"**The oculomotor system uses a prediction of the time at which the eye trajectory will cross the target, defined as the "eye crossing time" (TXE).** The eye crossing time, which depends on **both position error and velocity error**, is the criterion used to switch between smooth and saccadic pursuit, i.e., to trigger catch-up saccades." (de Brouwer, Yuksel, Blohm, Missal & Lefèvre JNP 2002)

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4. Calculation of $-EPE + (T_{XE} \times TV_{estim}) = AMP$

Estimated Target Displacement TD

Interceptive saccades

Exp Brain Res (2011) 110:133–147
DOI 10.1007/s00221-010-0191-9

RESEARCH ARTICLE

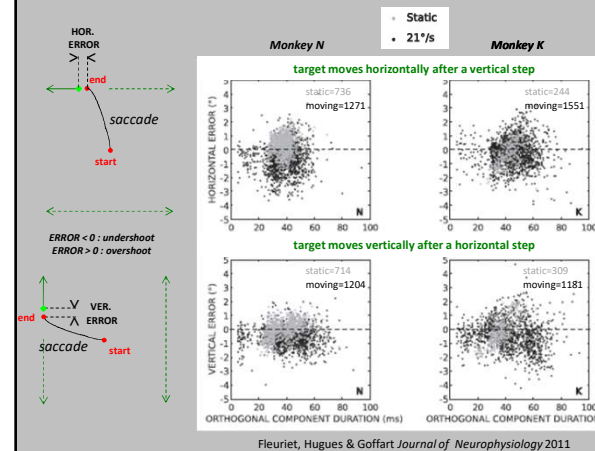
F. Khan · J. Petit · A. Grantyn · A. Berthoz

Predictive elements in ocular interception and tracking of a moving target by untrained cats

Abstract We presented a mechanical target moving at constant velocity to awake, nontrained, head-restrained cats, in order to study how naive mammals pursue objects moving at a high speed with their gaze. Eye movements were recorded while the target was moving in different directions at a constant velocity (20–80°/s) through the center of the visual field. We observed two oculomotor strategies: cats either made an **interception saccade (IS)** toward the target but opposite to its motion, or tracked it in the direction of motion. They used the interception strategy more frequently when the gaze position error at the onset of target motion was large, and the tracking strategy when it was small. Interception was always achieved by single saccades, which were faster than tracking saccades (TS). During tracking, cats generated sequences of two to six saccades separated by "smooth" eye movements. Tracking quality varied considerably from trial to trial. When the level of motivation was high, cats would track the target at 80% over up to 75% of the oculomotor range, with relatively small position errors. We compared ISs and TSs with respect to their metric properties and timing. The amplitudes of ISs positively correlated with position error existing 100 ms before saccade onset, but saccade vectors were directed to a point ahead of the target along the target's track. We conclude that, in programming the ISs, target motion is used to predict the future target position so as to assure a spatial lead of the gaze at the saccade end, instead of attempting a precise capture of the target. The amplitude of TSs did not depend on preceding position errors. TSs were usually small at the onset of the first saccade, as if cats would wait till the target arrived near the line of sight. A majority of primary TSs were initiated before the target arrived near the direction of gaze. Thus they had a direction, opposite to the position error sampled 100 ms before the saccade, but the same as the direction

ANOTHER CONCERN : claims that are supported by sparse and anecdotal observations !!!

Accuracy and precision of saccades



Comparable errors between saccades toward a static versus moving target

NO SPATIAL LEAD of endpoints for interceptive saccades

Fleuriet, Hugues & Goffart Journal of Neurophysiology 2011

Anecdotal observations made in untrained cats

Exp Brain Res (2011) 210:333–347
DOI 10.1007/s00221-010-0675-9

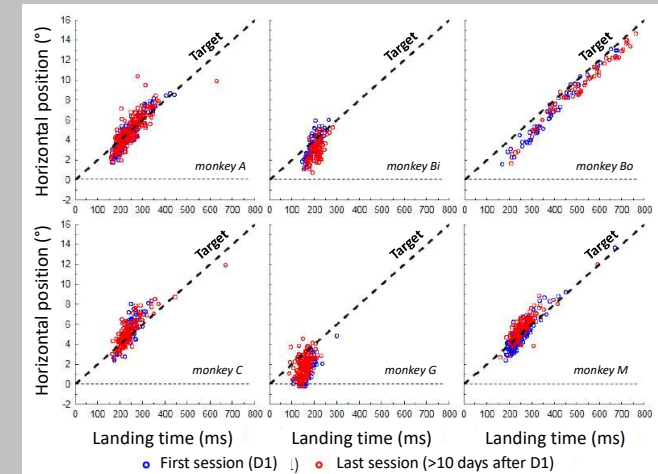
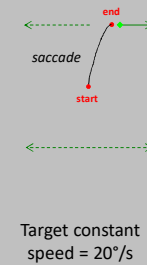
RESEARCH ARTICLE

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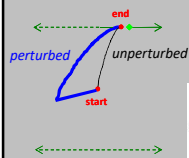
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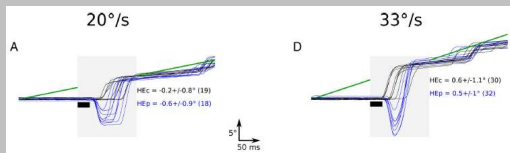
No spatial lead either in untrained monkeys



No spatial lead after perturbation



Microstimulation in the right deep Superior Colliculus (30ms 400Hz 12µA)



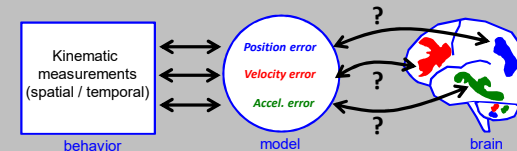
Fleurbaey & Goffart Journal of Neuroscience 2012

Contrary to the claim that interceptive saccades “would assure a spatial lead of the gaze at the saccade end instead of a precise capture of the target”, our observations indicate that interceptive saccades either precisely capture the target, where it is when it is there or undershoot the target (lag).



Dividers, physical quantities and arithmetic in the brain ?

QUESTIONING THE BRAIN-MODEL ISOMORPHISM



The fact that we measure and model the movement of the eyeball (a rigid body) with kinematic notions **does not imply** equivalence in the brain, and notably that the firing of neurons ought to “encode” (i.e., emit signals related to) amplitude, velocity or acceleration of the eye movement.

Another major concern

SPACE-TIME REPRESENTATION IN THE BRAIN. THE CEREBELLUM AS A PREDICTIVE SPACE-TIME METRIC TENSOR

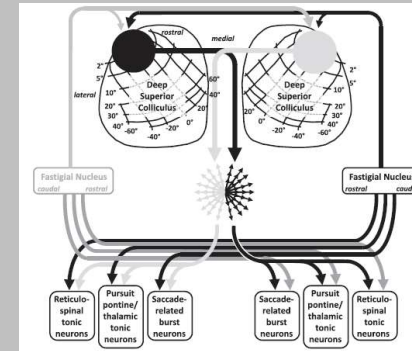
A. PELLIONISZ and R. LLINÁS
Department of Physiology and Biophysics, New York University Medical Center,
550 First Avenue, New York, NY 10016, U.S.A.

Understanding of brain function is often limited by the tacit acceptance of concepts known to be basically inappropriate. An example is the tenet that the brain, in its internal workings, utilizes space-time reference frames similar to those used in classical mechanics.

However, the utilization of separate systems of coordinates for space and time hinges upon the concept of simultaneity. Since within the brain there is no 'instantaneous' simultaneity agent comparable to the light, the classical usage of separate space and time coordinates is inapplicable in the case of describing the inner workings of the CNS.

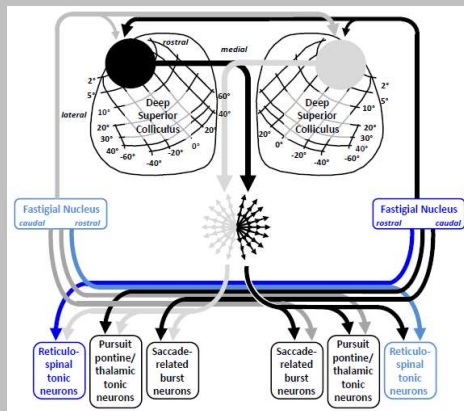
Neuroscience 1982

Alternative viewpoint



No movement = equilibrium
Movement = restoration of equilibrium

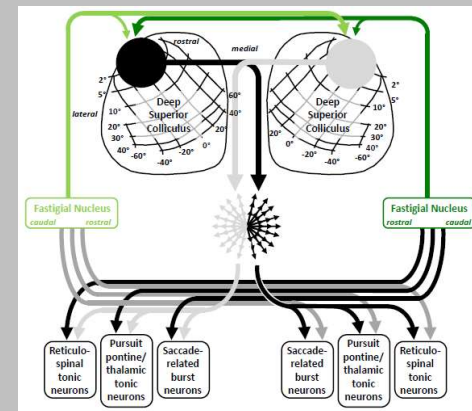
Head direction as equilibrium



Fastigio-reticulo-spinal perturbation
→ cervical dystonia

Progress in Brain Research 2019

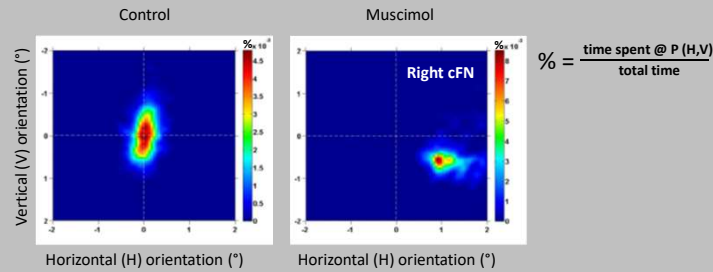
Gaze direction as equilibrium



Fastigio-collicular perturbation
→ fixation offset

Progress in Brain Research 2019

Fixation offset in the monkey

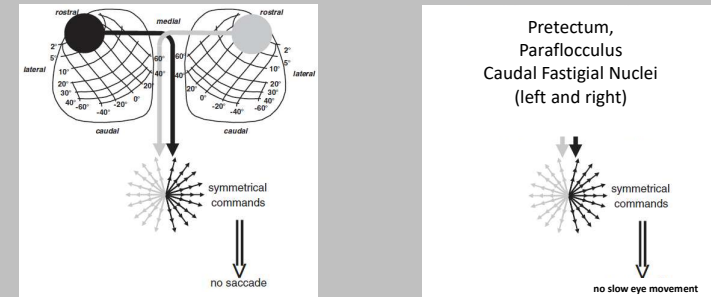


Gaze direction as multi-equilibrium

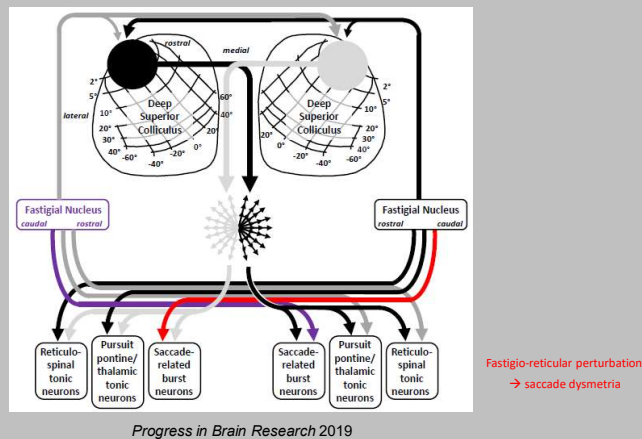
Multiple simultaneous equilibria

Two types of input drive the activity of motoneurons :

- * PHASIC (bursting) → saccade
- * TONIC (sustained) → glissade



Saccade as restoration of equilibrium



Herbert Spencer (1872) defended that the a priori forms of intelligence, like space, were inherited from evolution, encrypted in the neurophysiology :
"the space relations have been the same, not only for all men, all the primates and all the orders of mammals from which we descend, but also for all the orders of less elevated beings". They would be *"expressed in definite nerve structures, congenitally constituted to act in a certain way, and unable of acting in a different way"*.

Completed by ontogenetic adjustments, this phylogenetic adaptation would then consist of a kind of mimesis, an internalization of "laws" presumed to constrain the phenomenon in the physical world.

For **Konrad Lorenz** (1941), it would have *"given to our thought an innate structure that corresponds to a large extent to the reality of the external world ... Our forms of intuition and our categories adjust to what really exists in the same way as our foot adjusts to the ground or the thins of the fish to water"*.
 → theory of reflect, according to which thought only reflects the world.

Nowadays, the idea is diffused that the laws of classical mechanics are internalized in the functioning of the brain.

Alain Berthoz claims that *"the brain has internal models of Newton's laws"* (Simplicity, 2012).

Against this quasi-passive conception of intelligence and living forms, we can propose a more "combative" one, a thesis according to which cognition, physiology and even morphology are not mere representations, embodied copies of the external world ; they can be viewed as **counter-reactions, explorations of possibilities for expansion**, attempts to make sustainable paths through a medium delimited by a set of **constraints which are specific to each level of complexity**.

ACKNOWLEDGMENTS



András Pellionisz
PhD

Old dogmas and new axioms in brain theory

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There may be no more important task for theory in any branch of science than removing old dogmas – those that are proven inappropriate yet linger – and replacing them with new axioms. This task is acutely important in neuroscience, which is presently undergoing a metamorphosis from a largely descriptive (“soft”) science where the fundamental assumptions are taken for granted into an exact discipline with its own mathematized brain theory, in which case the axioms must be explicit. The process of identifying implicit fundamental assumptions, followed by the adoption of proper axioms and the removal of inappropriate dogmas, is a most difficult and often thankless job. The ground must nevertheless be cleared if one expects to build a sound, mathematical brain theory on the foundation of a newly established set of axioms.

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