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Neural processes underlying the foveation and tracking of a moving visual target

Laurent Goffart, PhD

Questions at the root of Science

How assemblies of neurons distributed throughout the brain enable a subject with the ability to localize and pursue an object situated in the physical world?

How to relate activities of microscopic elements (neurons) to macroscopic behavioral (kinematic) parameters?

What does this relation tell us?

How to relate events unfolding in mediums of different complexity order, mediums characterized by radically different constraints and temporalities?

The cerebral and physical mediums are not independent from each other:
- neuronal dysfunction → behavioral consequences
- repeated exposure to an environment → behavioral changes → changes in sensorimotor transformations
  (e.g. Bourrelly, Quinet, Cavanagh & Goffart. Journal of Neurophysiology 2016)
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 cerebral populations*
*two premotor input: PHASIC (burst) and TONIC*

- values > 0: rightward / upward
- value = 0: straight ahead
- values < 0: leftward / downward
Dividers, physical quantities and mathematics in the brain?

CIRCUIT FOR SACCADE

\[ \text{Motor Error} = \text{Desired} - \text{Current Positions} \]
\[ \text{Desired} - \text{Current Eye Displ.} \]
\[ \text{Target} - \text{Eye Displ.} \]

CIRCUIT FOR PURSUIT

\[ \text{RPE} = \text{retinal position error} \]
\[ \text{RAE} = \text{retinal acceleration error} \]
\[ \text{RVE} = \text{retinal velocity error} \]

Lisberger, Morris & Tychsen (1987)

When a model is adopted, results are often interpreted within its framework. If the data do not fit with the model predictions, some tweaks or smart adjustments can be made in the model.

But we can also ask ourselves:

Is there anything in the brain activity that would correspond to amplitude, duration and velocity?

This is a crucial question because we can search for such signals in the brain activity for a very long time, even an even longer time if these notions have no physiological substrate.

When evidence is found, we must also verify that the empirical data have not been distorted by statistical or analytical artifacts (e.g., coding of dynamic motor error in the SC, coding of eye velocity by premotor burst neurons, coding of saccade duration in the oculomotor vermis etc.).

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 an 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.

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

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Understanding brain functions is often limited by the tacit acceptance of concepts known to be basically inappropriate. An example is the brain's use of internal workings, utilizing space-time reference frames similar to those used in classical mechanics.

Moreover, the existence of separate regions of coordinate in space and time is one aspect of the concept of internal space-time frames. The cerebellum demonstrates similar properties compared to the brain, the classical usage of separate space and time coordinates is insupportable in the case of describing the nervous workings of the CND.
The fact that we measure and model the movement of the eyeball (a rigid body) with kinematic notions does not imply an 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.

Is it possible to study the neurophysiology of visually-guided eye movements without embedding kinematic notions within the brain functioning?

Looking at a visual target

Non-homogeneous retina

Foveal projection of target image requires tonic contraction of extraocular muscles → gaze direction
Foveal projection of target image requires tonic contraction of neck muscles → head direction

Looking at a visual target IS contracting multiple muscles

Reticulo-cerebellar interactions and the adjustment of eye and head orientations

Head direction as equilibrium
Cervical dystonia

*Muscimol (right cFN)*

Goffart & Pélisson J Neurophysiol 1998 (head free cat)
Quinet & Goffart J Neurophysiol 2005 (head free monkey)

Gaze direction as equilibrium

Fastigio-collicular perturbation → fixation offset

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Fixation offset in the monkey

Direction of fixational saccades

\[
\text{%} = \frac{\text{time spent @ P (H,V)}}{\text{total time}}
\]
Multiple simultaneous equilibria

Gaze direction as multi-equilibrium

Two types of input drive the activity of motoneurons:
* PHASIC (bursting) \(\rightarrow\) saccade
* TONIC (sustained) \(\rightarrow\) glissade

Pretectum, Paraflocculus, Caudal Fastigial Nuclei (left and right)

Saccade as restoration of equilibrium

Microstimulation (100Hz)
Control
Muscimol (right cFN)

Saccade dysmetria during cFN inhibition

Muscimol (right cFN) Microstimulation (100Hz)

Microstimulation (100Hz)
Control
Muscimol (right cFN)

Dysmetria of horizontal component due to the suppression of intrasaccadic burst

Modified from Kleine, Guan & Büttner, J Neurophysiol 2003
Horizontal saccade as restoration of equilibrium under fastigial control

For every saccade (horizontal, oblique or vertical), the left and right cFN regulate the balance of activity between excitatory input (EBNs) and inhibitory input (IBNs) to the motor and interneuronal neurons in the abducens nucleus (Goffart, Chen & Sparks, *J Neurophysiol* 2004).

MOVIE

Extending the bilateral hypothesis to pursuit (pursuit as sustained imbalance)

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Extending the bilateral hypothesis to pursuit (pursuit as sustained imbalance)

Journal of Neurophysiology 2018

Bourrelly, Quinet & Goffart. *Journal of Neurophysiology* 2018

Discontinuation of saccades and pursuit when the fastigial nucleus is inactivated (Signoret, 2018). Pursuit impairment due to asymmetry in bilateral NOT activity.

Perturbation \rightarrow slower pursuit

No alteration of pursuit latency (pursuit onset due to asymmetry in bilateral NOT activity).
SUMMARY: Bilateral hypothesis

Left & right Fastigial Nuclei

Nucleus Reticularis Gigantocellularis

NRG (RF)

rostral SC

PMRF

Gigantocellularis

F-reticulo-spinal n.

Fastigiospinal n.

Pontomedullary Reticular Formation

saccade-related n.

saccade-related n.

PNP / NRTP

heading

foveating
Summary: Bilateral hypothesis

Dysmetria of vertical component
Microstimulation outside the Fastigial Oculomotor Region (Hor)
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