Institute of Neuroscience, Newcastle University
Prof. Jenny Read
Newcastle, 2014 September 22

Brain processes for foveating a visual target here-and-now

Laurent Goffart, PhD

Space and time at the foundation of knowledge

“ What then are time and space ?

Are they real beings (existences) ?

Or, are they merely determinations or relations between things ?
And those relations, are they such that they would remain between things, even though they would never become objects of intuition ?

*Or, are they such that **they belong** only to the form of intuition, and consequently **to the subjective constitution of the mind**, without which these predicates of time and space could not be attached to any object ? ”*

Immanuel Kant
Critique of Pure Reason (1781)

Neurobiological foundations of space and time

<u>IF</u> *space and time are **a priori** and **necessary** representations that the mind uses to construct knowledge,*

(assuming that the neurobiology can explain the nature of the mind)

<u>THEN</u> *one should be able to find the neurobiological foundations of space and time*

(and THEREAFTER, better understand
- the nature of knowledge and
- how it is built upon interactions with the environment).

In the early XXth century, a mathematician-philosopher envisioned
how such a "kantian" space could be represented.

Space as a sensorimotor representation

*“The **representative space** … differs essentially from **geometrical space**.*
It is neither homogeneous nor isotropic; we cannot even say that it is of three dimensions.
It is often said that we "project" into geometrical space the objects of our external perception; that we "localize" them.
Now, has that any meaning, and if so what is that meaning? Does it mean that we represent to ourselves external objects in geometrical space?
Our representations are only the reproduction of our sensations; they cannot therefore be arranged in the same framework — that is to say, in representative space… Representative space is only an image of geometrical space, an image deformed by a kind of perspective.
When it is said, on the other hand, that we "localize" such an object in such a point of space, what does it mean?
***It simply means that we represent to ourselves the movements that must take place to reach that object. And it does not mean that to represent to ourselves these movements they must be projected into space, and that the concept of space must therefore pre-exist**”*

Henri Poincaré
La science et l’hypothèse (1902)

The orienting reaction (OR) as a probe to investigate the neural representations of "space"

The OR : a set of coordinated and organized muscle contractions / relaxations that lead to orient rapidly one (several) sensory organ(s) toward the location of a detected event.

1) ORs are relatively accurate

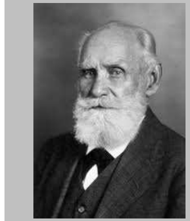
→ to the ***physical location*** of an object corresponds the ***flow of neural activity***
from the time when the object is detected
to the time when the associated orienting reaction ends.

2) ORs are accurate over a large range of different physical locations

→ different locations can be ***ordered*** along dimensions, e.g., the H and V spatial extents. Both H and V dimensions are commonly considered as driven by a topographically-organized map of labeled lines (superior colliculus/optic tectum).

→ this map is an inferred entity as ***one single target is aimed at a time***

The orienting response and knowledge acquisition



> *"It is this reflex which brings about the* ***immediate response*** *in man and animals* ***to*** *the slightest* ***changes*** *in the world around them, so that they immediately orientate their appropriate receptor-organ in accordance with the perceptible quality in the agent bringing about the change, making full investigation of it.*
>
> *The biological significance of this reflex is obvious. If the animal were not provided with such a reflex its life would hang at every moment by a thread.*
>
> ***In man, this reflex has been greatly developed in its highest form, by inquisitiveness*** *– the parent of that scientific method through which we hope one day to come to a true orientation in knowledge of the world around us."*

Ivan P. Pavlov
Conditioned reflexes (1927)

Morphological diversity & Functional regularities

Across living animals, several morphological differences are observed in :
- the sensory organs (retina, cochlea, olfactory bulb, etc.),
- the motor plants (extra-ocular and neck muscles, geometry etc.),
- the neural circuits

that are involved in transforming a sensory event into an OR.

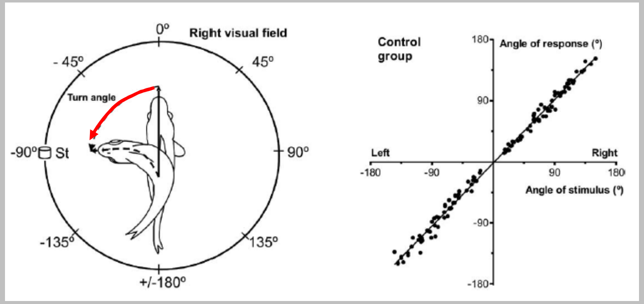
In spite of this diversity, some ***regularities*** are found :
- within a particular animal,
- within a species and
- between species

in the temporal and spatial structure of the OR.

Temporal regularity : the OR is always extremely rapid (saccadic = ballistic-like), even after a paresis of the oculomotor system (head saccades).

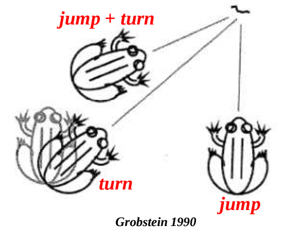
Spatial regularity: the spatial properties of the OR fit with the spatial extent of the environment with a variability that is relatively delimited .

Orienting body movement in the goldfish



Torres et al. Brain Res. Bull. 2005

Orienting body movement
in the frog



Grobstein 1990

Result of first reaction :
orient the gaze
(field of visuomotor interactions)
toward the target

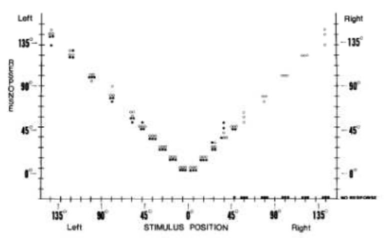
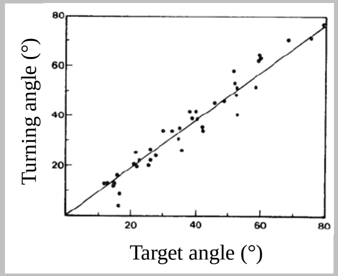


Fig. 1. Orienting behavior of a frog before and after section of the right optic nerve. Stimulus positions are shown by the short lines on the horizontal axis and are defined as number of degrees to the right or left around the animal from the snout. Response angles are shown on the vertical axis. Stimuli to the right elicited turns to the right (right vertical axis); those to the left elicited turns to the left (left vertical axes). Each symbol corresponds to one trial; symbols on the horizontal axis show trials on which the frog failed to respond. Open symbols, before optic nerve section; closed symbols, after optic nerve section.

Kostyk & Grobstein 1982

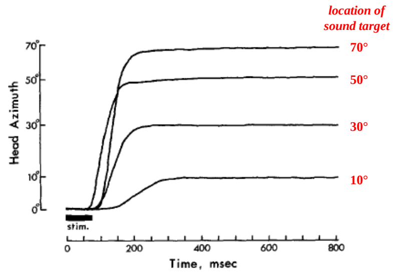
Orienting head movement
in the salamander

Schülert & Dicke J. Exp Biol 2002



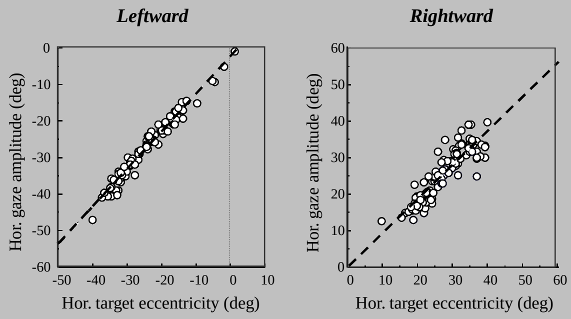
Werner & Himstedt
Zool. Jb. Physiol. 1985

Orienting head movement
in the barn owl



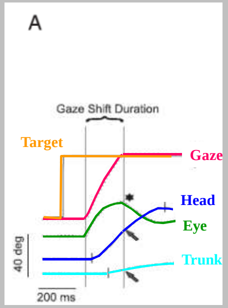
Knudsen, Blasdel & Konishi JCP 1979

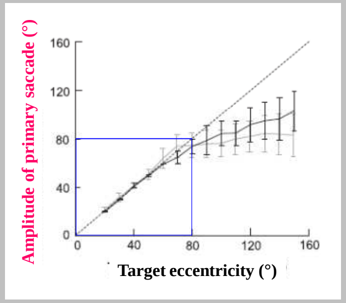
Orienting gaze shift
in the cat (head free)



modified from Goffart & Pélisson JNP 1994

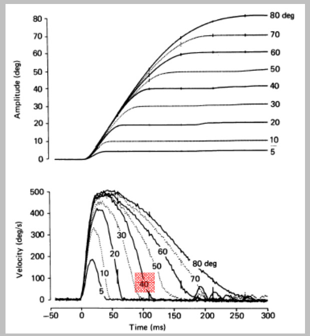
Orienting gaze shift
in the monkey (head free)

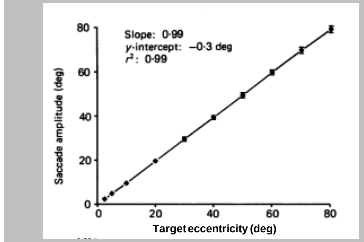




McCluskey & Cullen JNP 2007

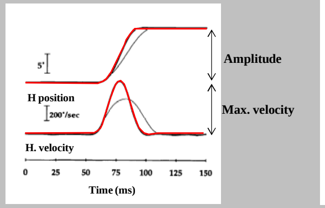
Eye saccades in the human subject



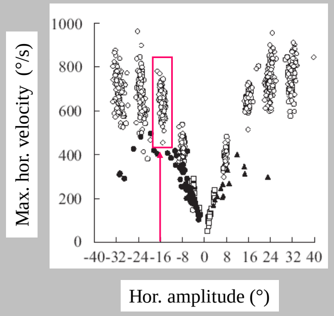


Collewijn et al JP 1988

Robustness : spatial accuracy is maintained
in spite of variable saccade dynamics



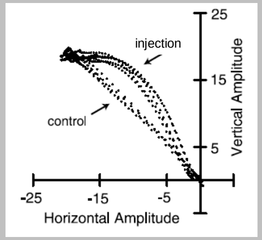
Stanford, Freedman & Sparks JNP 1996



Quinet & Goffart JNP 2009

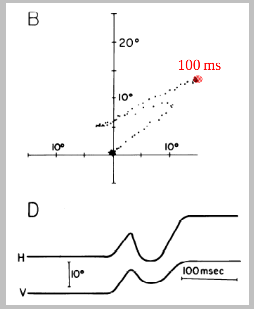
Robustness : spatial accuracy is maintained
even after experimental perturbations

Pharmacological inactivation
(Pontine Reticular Formation)



Barton, Nelson, Gandhi & Sparks JNP 2003

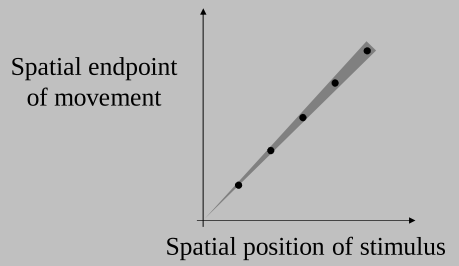
Brief electrical microstimulation
(deep Superior Colliculus)



Sparks & Mays JNP 1983

Spatial accuracy is robust

In spite of the diversity of sensory organs, motor devices and nervous systems and variable execution (velocity, eye-head-body coupling, perturbation)

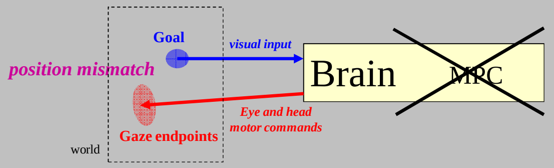


What are the (neuro) biological foundations of this relationship ?

The medio-posterior cerebellum (MPC) and the control of orienting gaze shifts

Dysfunction of MPC leads to gaze **dysmetria** i.e. it alters the spatial congruence between :

- the location of a visual event
- the endpoint of gaze shifts towards it



The medio-posterior cerebellum

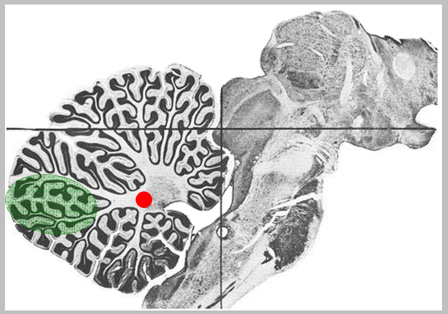
Lobules VIc-VII

caudal Fastigial Nuclei
(Fastigial Oculomotor Regions)

Saccade-related activity

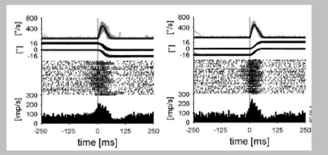
Pursuit-related activity

Vergence-related activity

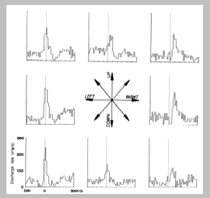


Saccade-related activity in the caudal fastigial nucleus

(head-restrained monkey)



Kleine, Guan & Büttner JNP 2003

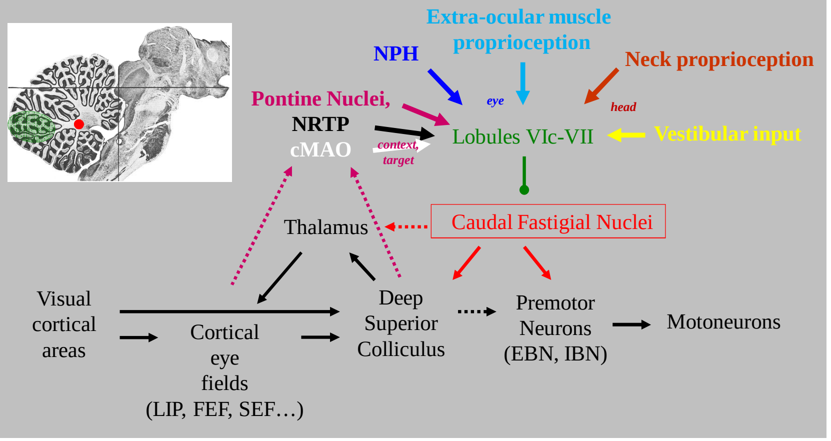


Ohtsuka & Noda JNP 1991

1. Burst of action potentials for all saccades regardless of the amplitude and direction
2. Sustained discharge during inter-saccadic intervals

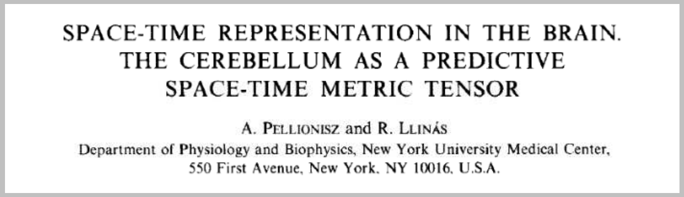
Inputs with different dynamics

(different delays, temporal patterns etc…)


Extra-ocular muscle proprioception
NPH
Neck proprioception
Pontine Nuclei,
NRTP
cMAO
eye
head
Lobules VIc-VII
Vestibular input
context, target
Thalamus
Caudal Fastigial Nuclei
Visual cortical areas
Cortical eye fields (LIP, FEF, SEF…)
Deep Superior Colliculus
Premotor Neurons (EBN, IBN)
Motoneurons

"All models are wrong, but some are useful"

George E.P. Box

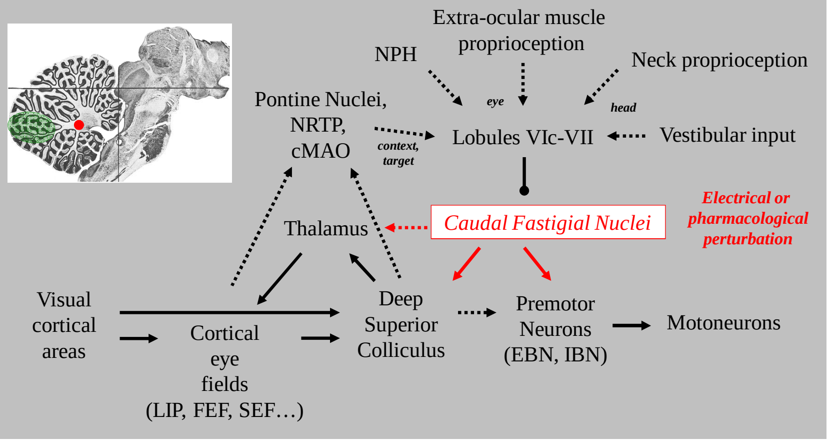

SPACE-TIME REPRESENTATION IN THE BRAIN.
THE CEREBELLUM AS A PREDICTIVE
SPACE-TIME METRIC TENSOR

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.

*"The cerebellum acts as a metric tensor that establishes **coincidences** of goal-directed movements **in space-time** with external targets"*

Methodological approach : perturbation

(establishing causal relationships)


Extra-ocular muscle proprioception
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Pontine Nuclei,
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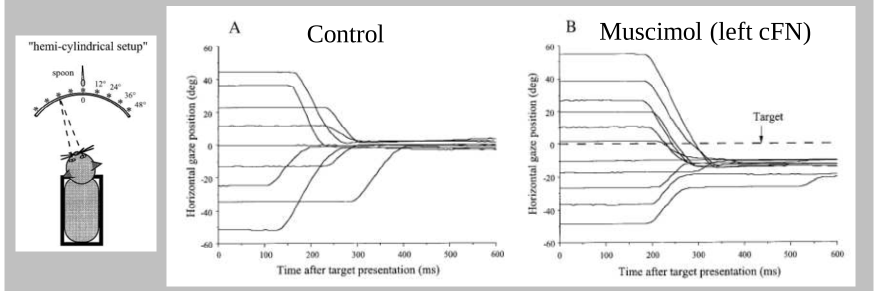
eye
head
Lobules VIc-VII
Vestibular input
context, target
Thalamus
Caudal Fastigial Nuclei
Electrical or pharmacological perturbation
Visual cortical areas
Cortical eye fields (LIP, FEF, SEF…)
Deep Superior Colliculus
Premotor Neurons (EBN, IBN)
Motoneurons

Ipsilesional and contralesional gaze shifts

Muscimol injection in the left cFN (0.3 µl; 1µg/µl,cat I)

Muscimol injection in the left cFN (0.3 µg)

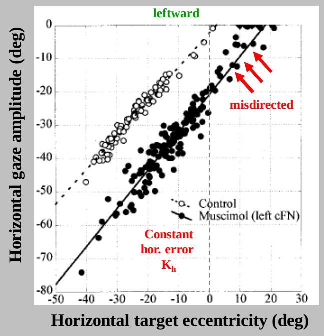


modified from Goffart & Pélisson JNP 1998

Gaze dysmetria

Muscimol injection in the left cFN (0.3 µl; 1µg/µl,cat G)

Ipsilesional movements

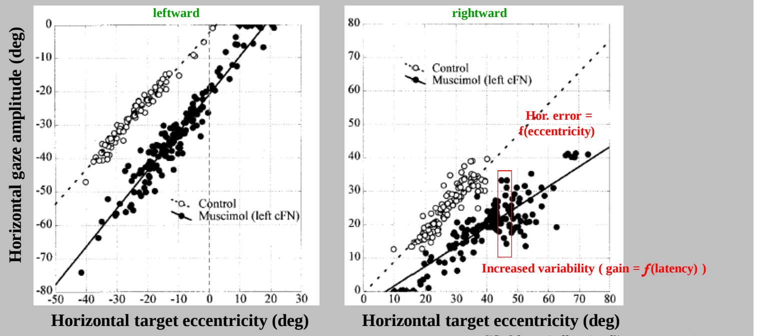


modified from Goffart & Pélisson JNP 1998

Gaze dysmetria

Muscimol injection in the left cFN (0.3 µl; 1µg/µl,cat G)

Ipsilesional movements **Contralesional movements**

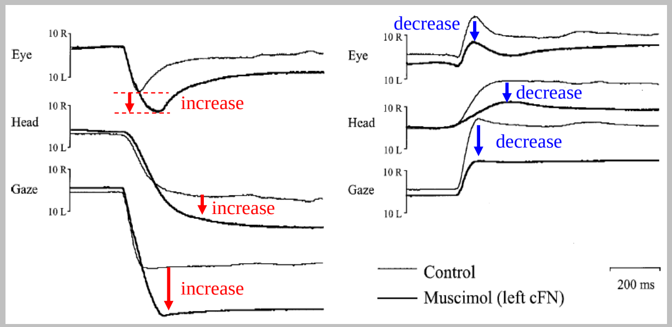


modified from Goffart & Pélisson JNP 1998
(see also Gofffart & Pélisson JP 1997)

Dysmetria affects eye and head movements

Muscimol injection in the left cFN (0.3 µl; 1µg/µl,cat G)

Ipsilesional **HYPER**metria Contralesional **HYPO**metria

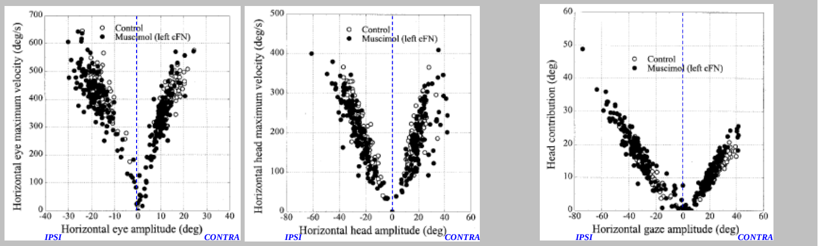


modified from Goffart, Pélisson & Guillaume JNP 1998

No sign of movement execution disorder

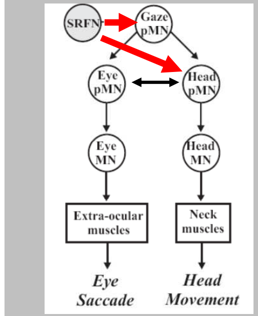
Muscimol injection in the left cFN (0.3 µl; 1µg/µl,cat G)

Eye velocity **Head velocity** **Eye-head coupling**



modified from Goffart, Pélisson & Guillaume. JNP 1998

Cat



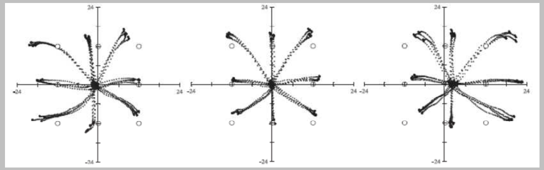
- Gaze dysmetria due to dysmetric **eye + head**
- Eye/head velocity **unchanged**
- Eye/head coupling **unchanged**

Goffart & Pélisson JP London 1997
Goffart & Pélisson JNP 1994, 1998
Goffart et al. JNP 1998a,b

Observations in the head-fixed monkey

target LEDs @ 145 cm : 0.25° visual angle, mesopic conditions, 0.4 µl (1µg/µl)

Muscimol (left cFN) **Control** **Muscimol (right cFN)**



Goffart, Chen & Sparks, JNP 2004

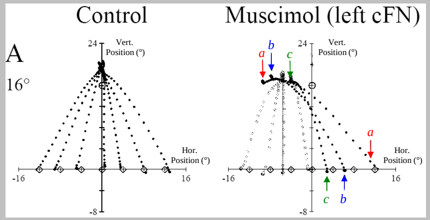
Ipsilesional saccades : horizontal component is **<u>hyper</u>**metric

Contralesional saccades : horizontal component is **<u>hypo</u>**metric

like in the head-unrestrained cat

Horizontal error is not constant

unlike the head-unrestrained cat

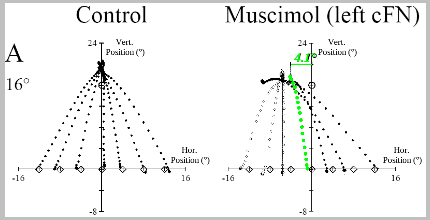


modified from Goffart, Chen & Sparks JNP 2004

Hor. Error *saccade a* > **Hor. Error** *saccade b* > **Hor. Error** *saccade c*

Horizontal error is not constant

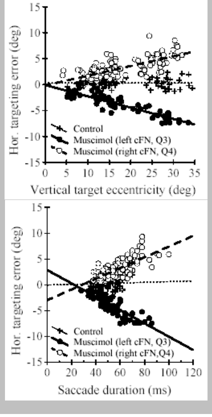
unlike the head-unrestrained cat



modified from Goffart, Chen & Sparks JNP 2004

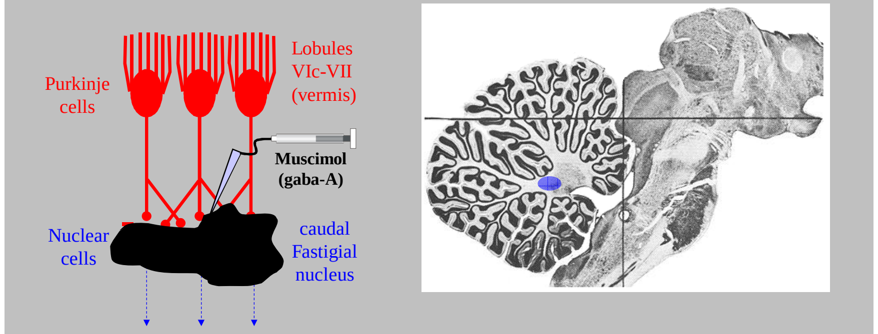
Hor. error. = *ƒ*(target eccentricity)
ƒ(saccade duration)

Vertical saccades



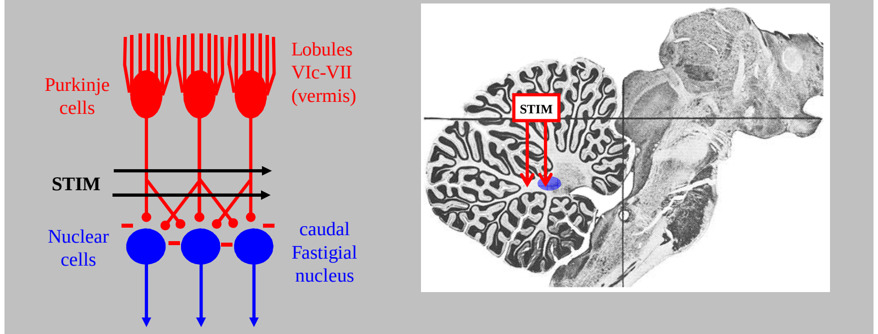
Impaired planning or execution ?

(pre- or intra-saccadic disorder ?)



Duration of inactivation ~ 2-3 hours :
This long-lasting perturbation does not allow deficits that are presaccadic to be distinguished from those occurring during saccade execution

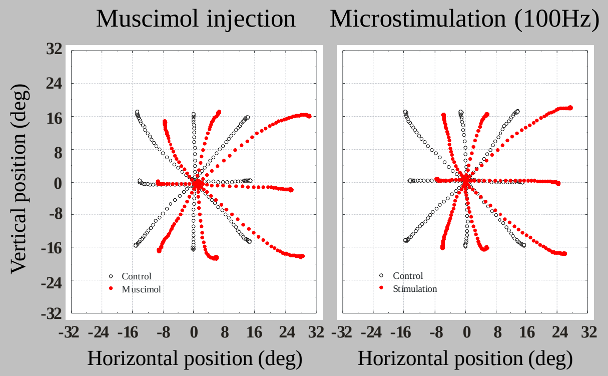
Inhibition of cFN activity with electrical microstimulation



Purkinje cells inhibit cFN neurons with Gaba-A as a neurotransmitter.
By stimulating their axons, one should be able to mimics, with a microstimulation train, the effects of muscimol on saccade accuracy.

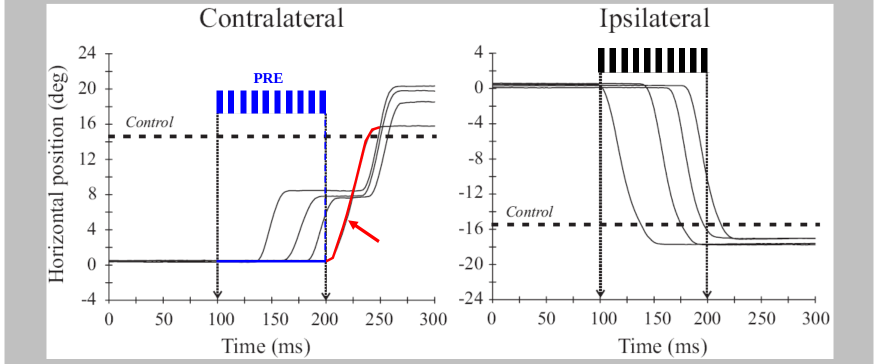
Inhibition of cFN

Right cFN (rebound saccades removed)



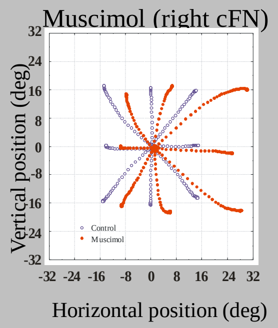
Time window of the perturbation

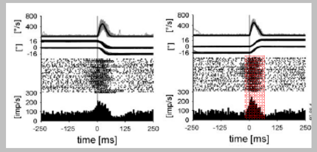
left caudal Fastigial Nucleus



Goffart & Quinet in preparation

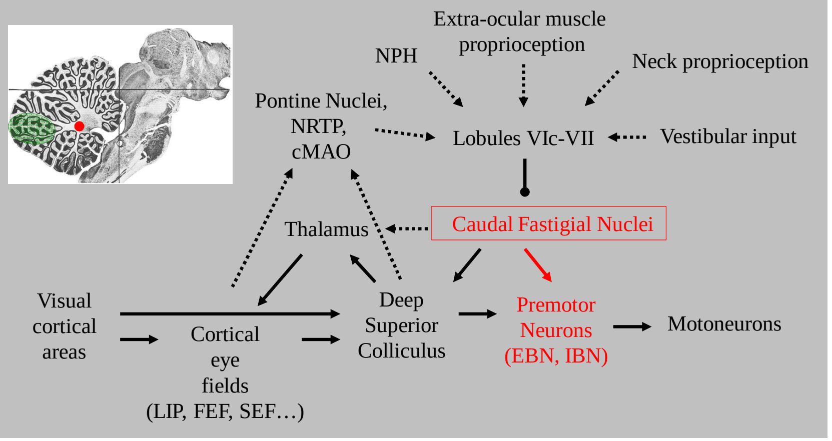
Horizontal dysmetria is due to the unilateral suppression of saccade-related bursts





modified from Kleine, Guan & Büttner JNP 2003

Fastigio-reticular projections and the cerebellar control of saccade amplitude



Extra-ocular muscle proprioception

NPH

Neck proprioception

Pontine Nuclei, NRTP, cMAO

Lobules VIc-VII

Vestibular input

Thalamus

Caudal Fastigial Nuclei

Visual cortical areas

Cortical eye fields (LIP, FEF, SEF…)

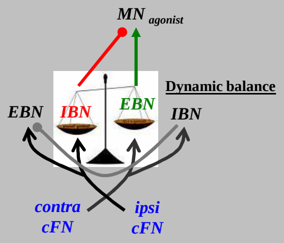
Deep Superior Colliculus

Premotor Neurons (EBN, IBN)

Motoneurons

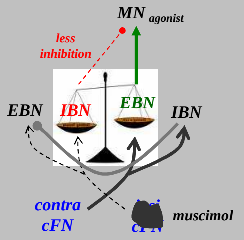
Bilateral hypothesis

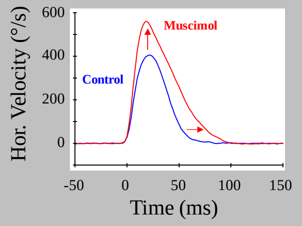
For every saccade (horizontal, oblique or vertical), the left and right cFN regulates the balance of activity between excitatory input (EBNs) and inhibitory input (IBNs)



Bilateral hypothesis

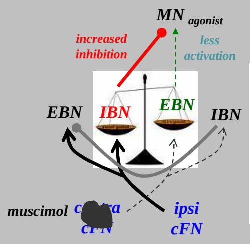
Ipsilesional hypermetria

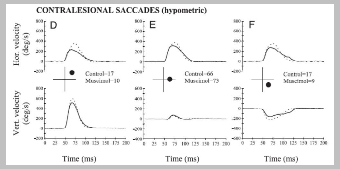




Bilateral hypothesis

Contralesional hypometria

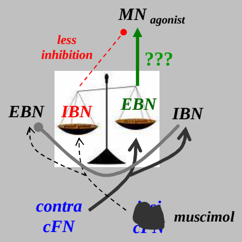


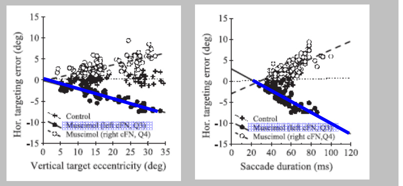


modified from Goffart, Chen & Sparks JNP 2004

Bilateral hypothesis

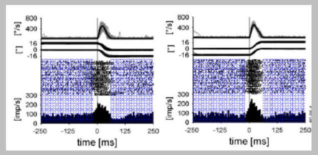
Ipsipulsion of vertical saccades



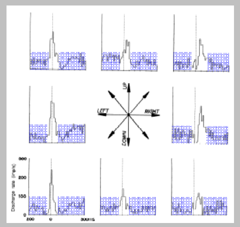


modified from Goffart, Chen & Sparks JNP 2004

What about the sustained activity in cFN ?



Kleine, Guan & Büttner JNP 2003



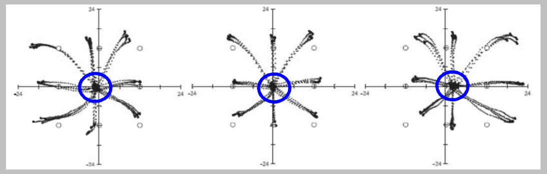
Ohtsuka & Noda JNP 1991

Ipsilesional fixation offset

like in the head-unrestrained cat

target LEDs @ 145 cm : 0.25° visual angle, mesopic conditions

Muscimol (left cFN) **Control** **Muscimol (right cFN)**

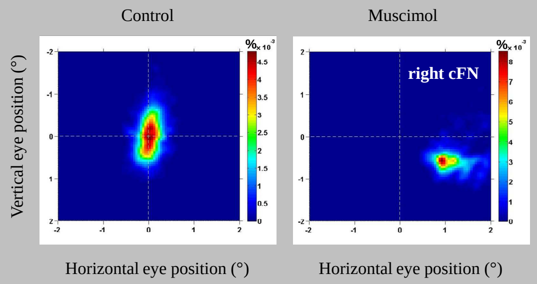


Goffart, Chen & Sparks, JNP 2004

Fixation offset : shift in the scatter of eye positions during fixation

Fixation offset : spatio-temporal map

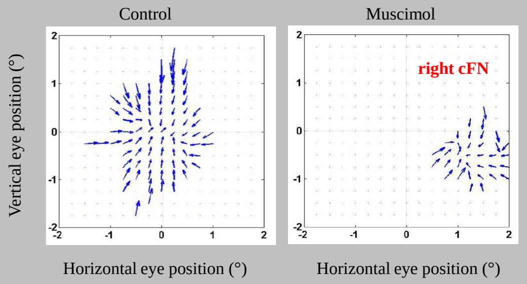
Monkey B



$$\% = \frac{\textbf{time spent at P (X,Y)}}{\textbf{total time}}$$

Directional field of fixational saccades

Monkey B

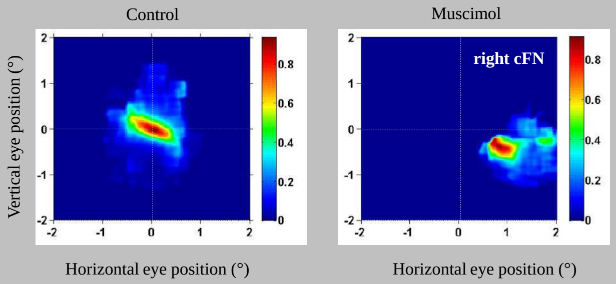


Bin width 0.375°
(N > 5 fixational saccades)

Attractor

Directional field : zone of maximum variance

Monkey B



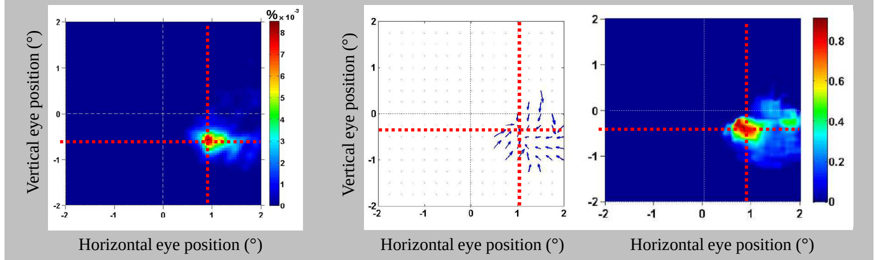
V = Variance
= 1- L

Bin width 0.375°
(N > 5 saccades)

Unstable attractor

Change in the oculomotor encoding of a foveal target ?

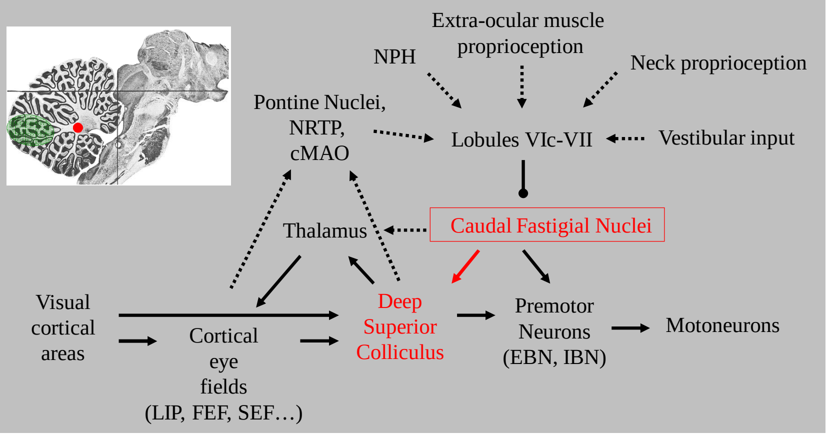
new zone of maximum time spent | **new zone of convergence** | **new zone of maximum variance**



J Neurophysiol 103: 1988–2001, 2010.
First published February 3, 2010; doi:10.1152/jn.00771.2009.

Fastigial Oculomotor Region and the Control of Foveation During Fixation

Lorenzo Guerrasio,[1] Julie Quinet,[2] Ulrich Büttner,[1] and Laurent Goffart[3]



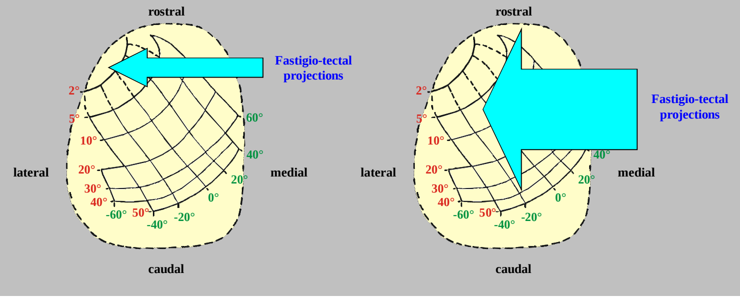
Behavior and neuroanatomy

In the monkey, a spatial deficit similar to that observed in the cat, is observed
when one considers the microsaccades generated when a visual target is being fixated.

This distinction could result from differences in the extent of fastigio-tectal projections.

Rhesus macaque
(May et al. *Neuroscience* 1990)

Cat



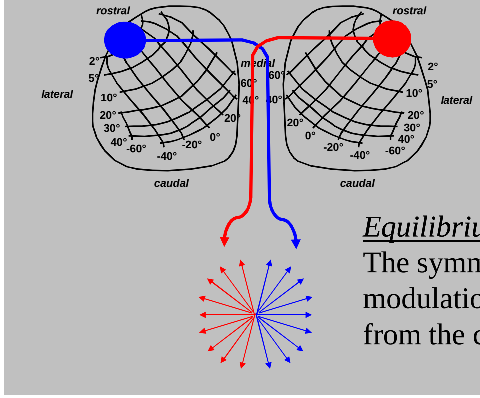
If the fixation offset corresponds to an
altered encoding of foveal target,
what is visual fixation ?

Visual Fixation as Equilibrium: Evidence from Superior Colliculus Inactivation

Laurent Goffart,[1] Ziad M. Hafed,[2] and Richard J. Krauzlis[3,4]

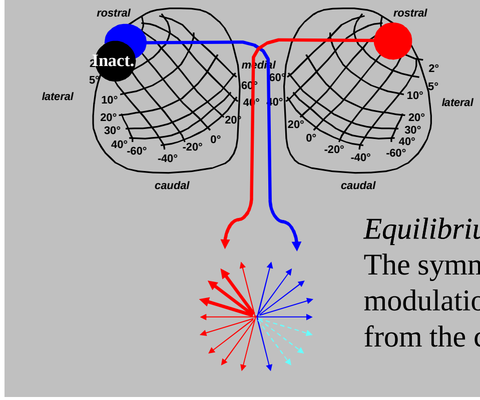
[1]Institut de Neurosciences de la Timone, UMR 7289, Centre National de la Recherche Scientifique, Aix-Marseille Universités, 13385 Marseille, France, [2]Werner Reichardt Centre for Integrative Neuroscience, 72076 Tuebingen, Germany, [3]Systems Neurobiology Laboratory, Salk Institute for Biological Studies, La Jolla, California 92037, and [4]Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, Maryland 20892

Journal of Neuroscience 2012



__Equilibrium requires symmetry__ :
The symmetry is acheived by
modulations exerted by projections
from the cFN to the brainstem

Experimental prediction
after muscimol injection in the rostral SC



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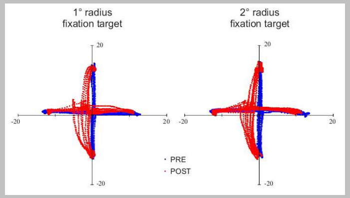
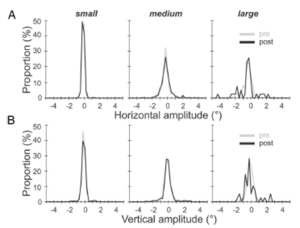


Ipsilesional fixation offset
Saccades to peripheral targets are accurate

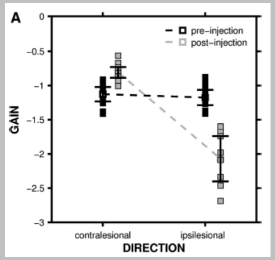


No asymmetry in the amplitude of fixational saccades

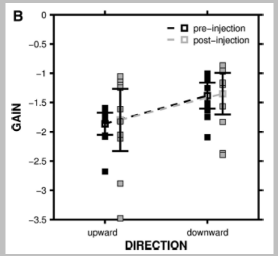
Goffart, Hafed & Krauzlis JN 2012

Asymmetry in the hor. ampl. of fixational saccades
after muscimol injection in the caudal FN

HORIZONTAL



VERTICAL

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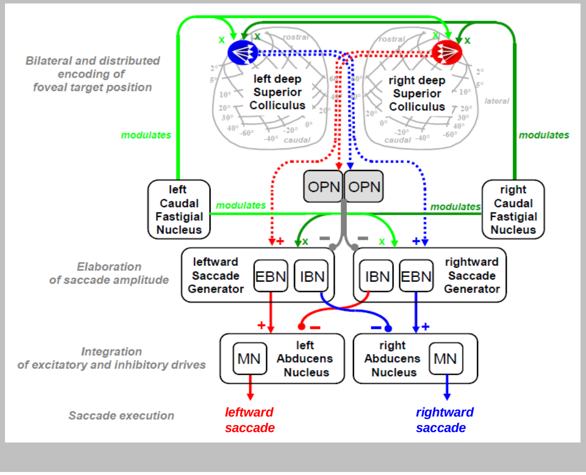
Fastigial Oculomotor Region and the Control of Foveation During Fixation

Lorenzo Guerrasio,[1] Julie Quinet,[2] Ulrich Büttner,[1] and Laurent Goffart[3]

Fastigial control of equilibria for foveation


Bilateral and distributed encoding of foveal target position

left deep Superior Colliculus

right deep Superior Colliculus

modulates

left Caudal Fastigial Nucleus

OPN OPN

right Caudal Fastigial Nucleus

Elaboration of saccade amplitude

leftward Saccade Generator EBN IBN

IBN EBN **rightward Saccade Generator**

Integration of excitatory and inhibitory drives

MN **left Abducens Nucleus**

right Abducens Nucleus MN

Saccade execution

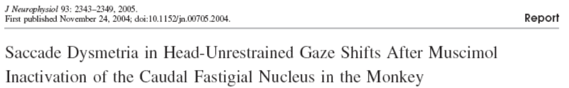
leftward saccade

rightward saccade

In the head-unrestrained monkey, gaze dysmetria is due to dysmetric saccadic eye movements

unlike the head-unrestrained cat

Quinet & Goffart JNP 2005



J Neurophysiol 93: 2343–2349, 2005.
First published November 24, 2004; doi:10.1152/jn.00705.2004.

Report

Saccade Dysmetria in Head-Unrestrained Gaze Shifts After Muscimol Inactivation of the Caudal Fastigial Nucleus in the Monkey

Quinet & Goffart JNP 2007

J Neurophysiol 98: 3269–3283, 2007.
First published October 10, 2007; doi:10.1152/jn.00741.2007.

Head-Unrestrained Gaze Shifts After Muscimol Injection in the Caudal Fastigial Nucleus of the Monkey

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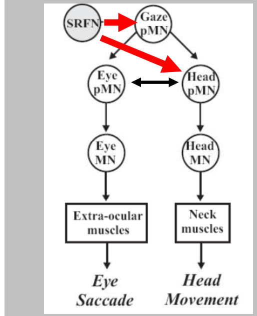
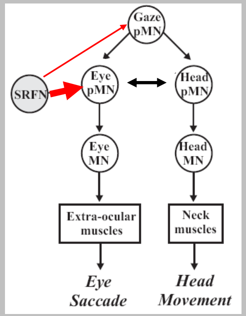
Cat



- Gaze dysmetria due to dysmetric **eye + head**
- Eye/head velocity **unchanged**
- Eye/head coupling **unchanged**

Goffart & Pélisson JP London 1997
Goffart & Pélisson JNP 1994, 1998
Goffart et al. JNP 1998a,b

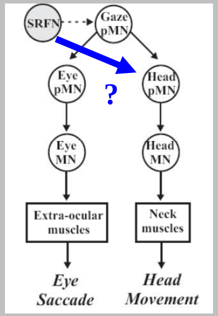
Primate



- Gaze dysmetria due to dysmetric **eye**
- Eye velocity **changed,** head velocity **unchanged**
- Eye/head coupling **changed**

Robinson et al. JCN 1994 (anatomy)
Quinet & Goffart JNP 2005, 2007 (inactivation)
Quinet & Goffart JNP 2009 (microstimulation)
Guerrasio, Quinet, Büttner & Goffart JNP 2010 (inactivation)
Fuchs et al JNP 2010 (unit recordings)

Rodent, Amphibian



- *Gaze dysmetria due to dysmetric **head ?***
- ***Head velocity changed**, eye unchanged **?***
- *Eye/head coupling changed **?***

James M. Bower’s theory of cerebellar control of sensory data acquisition

“The cerebellum is specifically involved in monitoring and adjusting the acquisition of most of the sensory data on which the rest of the nervous system depends.”
James M. Bower *International Review of Neurobiology* 41: 489-513, 1997

Adapted to our paradigm :

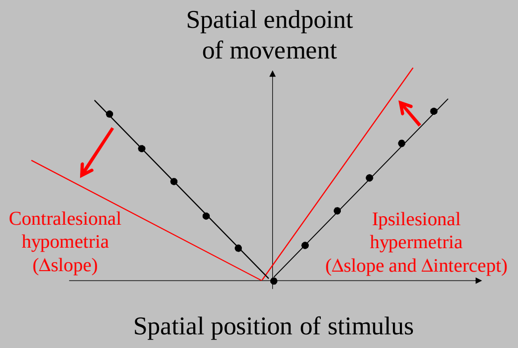
The medio-posterior cerebellum (MPC) is involved in orienting the ***primary sensory apparatus***.

*More specifically, the MPC would **compensate for intra- and inter-specific morphological variability***
- in the sensory organs used for detecting events (afferents) and
- in the motor plants (efferents) used for orienting toward them.

Experimental prediction :

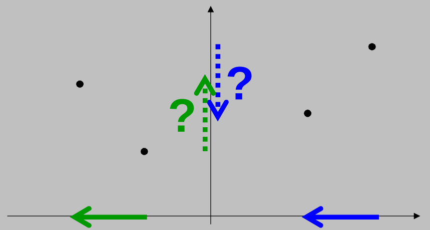
Dysfunction of MPC in species where the primary sensory apparatus is transported by the head (e.g.,Salamander, Mice etc) would lead to a deficit in orienting the head toward a target (no eye dysmetria).

Cerebellar control of horizontal saccade accuracy



Interceptive saccades are accurate

Spatiotemporal endpoint
of movement



Spatiotemporal position of stimulus

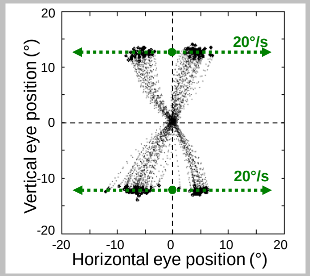
Continuous target motion in the world ⇏ ? ***? continuous ?*** change in its neural image in the brain

The *hic-et-nunc* (here-and-now) of saccade endpoints

Animals can make saccadic eye movements to visually intercept the trajectory of a moving object and foveate it ***at the right place and time***, and initiate its pursuit.

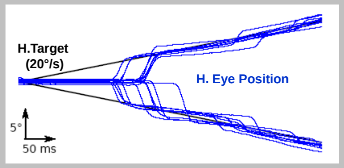
Such interceptive saccades indicate that, in spite of variable sensorimotor delays, the brain activity is able to estimate the ***hic-et-nunc*** **(here-and-now)** coordinates of a target, at least at the time of saccade landing.

Saccades toward a moving target

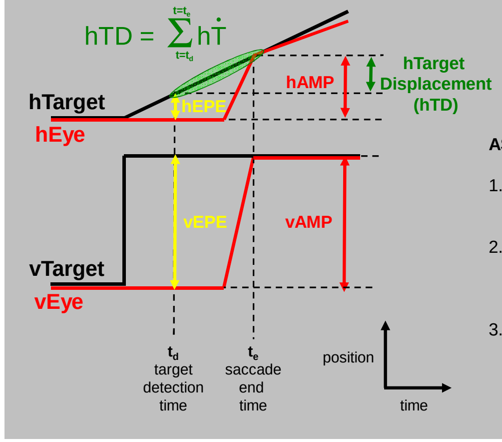


Target : gaussian-blurred disk
(0.5° diameter)

Horizontal component



The dual-drive hypothesis

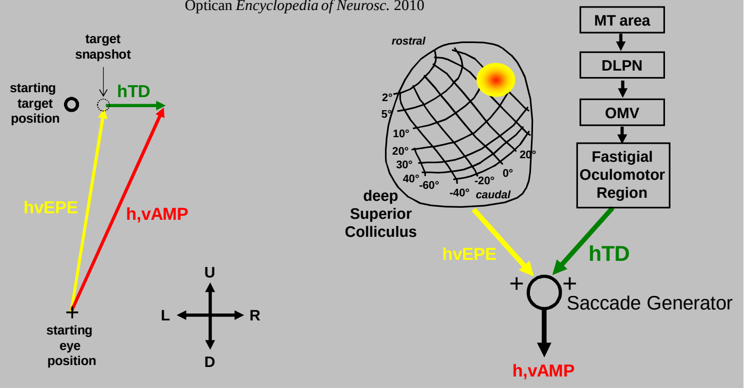


ASSUMPTIONS :

1. Snapshot of **Eye Position Error** (EPE)
   → discrete sampling
2. Estimate of **Target Displacement** (TD)
   → time window delimited by discrete events
3. **AMP** = **EPE** + **TD** (additive hypothesis)

The dual-drive hypothesis

Keller et al. *JNP* 1996
Optican & Quaia *ANYAS* 2002
Optican *Encyclopedia of Neurosc.* 2010

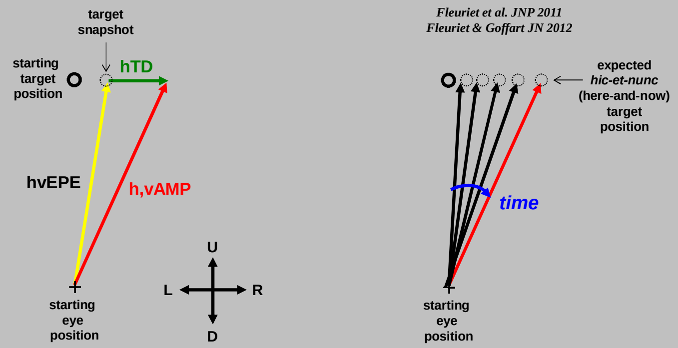


An alternative hypothesis

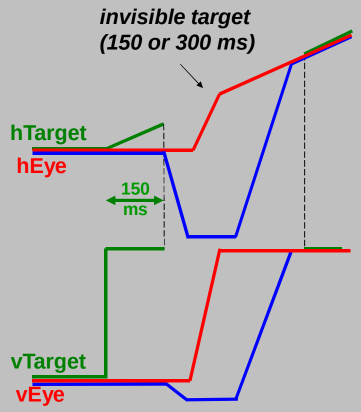
The 'dual drive' hypothesis

The 'dynamic remapping' or 'here-and-now' hypothesis

Fleuriet et al. JNP 2011
Fleuriet & Goffart JN 2012

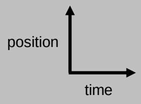


Visual feedback is removed



IF the saccade goal = *here-and-now* target position

THEN change in eye position and added delay should be taken into account (accurate saccades)

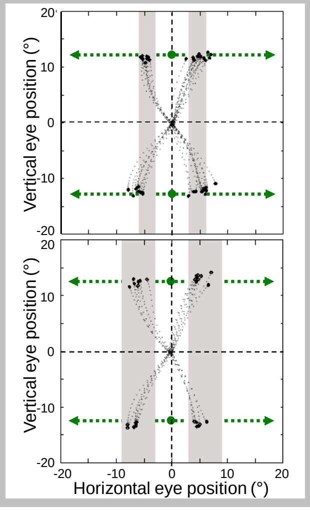


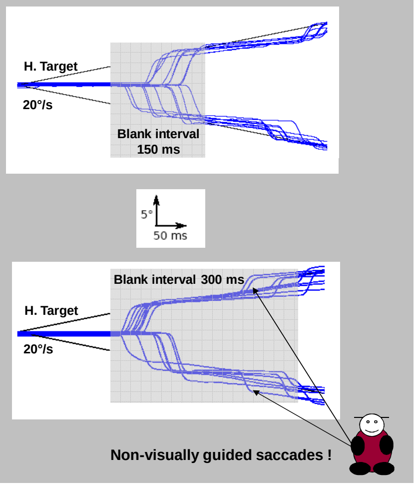
Saccadic interception of an occluded target

150ms blank

Target : gaussian-blurred disk (0.5° diameter)

300ms blank

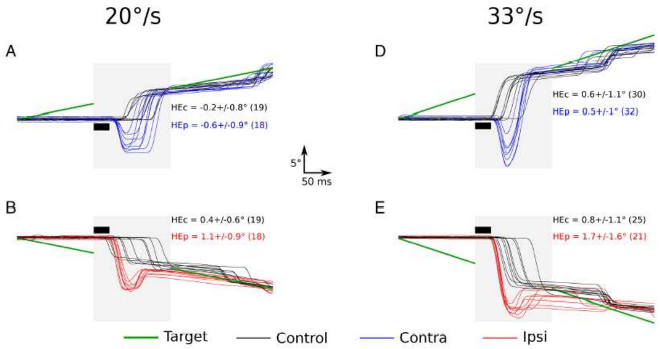




Non-visually guided saccades !

Perturbation of interceptive saccades

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



Fleuriet & Goffart JN 2012

Conclusions

A visual event undergoes a “spatio-temporal blurring” when the activity it evokes onto the retina propagates toward the oculomotor system (Pellionisz & Llinas 1982).

In spite of this blurring, the here-and-now coordinates of the target can ***in fine*** be estimated.

Our study shows that this neural estimate is robust enough for animals to capture the target even after an unexpected spatiotemporal perturbation (i.e., a change in eye position and its associated delay).

WORKING HYPOTHESIS : the gaze direction is driven by a ***flow of expected target positions***

No neural encoding of *future* target position (no predictive coding) but of expected here-and-now target position

Saccades are driven by a *dynamic mnemonic flow* which is temporally unfolded

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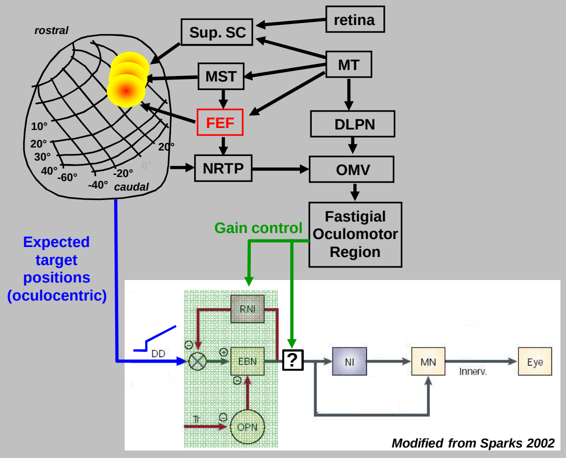
“Dynamic remapping” hypothesis



Modified from Sparks 2002

Conclusions

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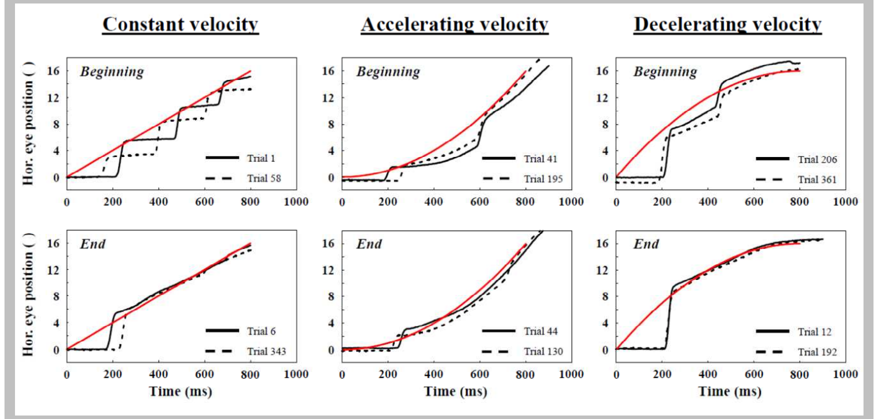
No neural encoding of *future* target position (no predictive coding) but of expected here-and-now target position

Saccades are driven by a ***dynamic mnemonic flow*** that is temporally unfolded

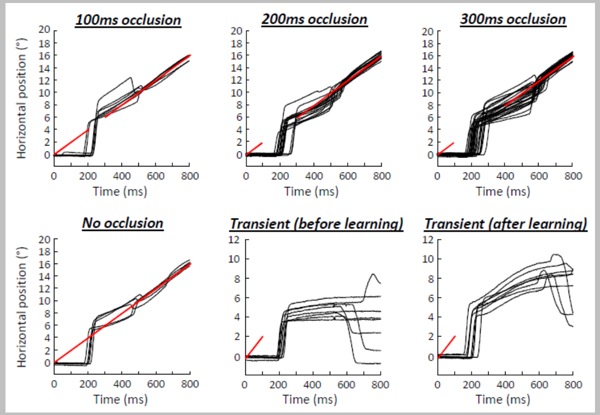
This flow is an “internal model” of target trajectory that has been learned and embodied (***dynamic morphing***)

Dynamic morphing



Bourrelly, Quinet & Goffart SFN 2013

Learning the trajectory of a briefly occluded target



Quinet, Bourrelly & Goffart SFN 2013

Brain and geometry

"The properties of time are only those of clocks, like the properties of space are only those of measuring instruments"

"In fact, it [space] is amorphous, it is a flabby form, with no rigidity, that can be applied to anything; it has no intrinsic properties; doing geometry is studying the properties of our instruments"

Henri Poincaré
Dernières pensées (1917)

"It appears that the parallel, distributed structuro-functional features of neural networks do furnish the CNS with an innate a priori propensity to implement geometries."

Pellionisz & Llinas (1982)

Acknowledgments

Experiments in the caudal Fastigial Nucleus

Head-free cat	***Head-restrained monkey***		***Head-free monkey***
Denis Pélisson, PhD	David L. Sparks, PhD	Lorenzo Guerrasio, PhD	Julie Quinet, PhD
Alain Guillaume, PhD	Longtang L. Chen, PhD	Ulrich Büttner, MD PhD	

Experiments in the deep Superior Colliculus (monkey)

Ziad M. Hafed, PhD
Rich J. Krauzlis, PhD
Jérome Fleuriet, PhD

Behavioral experiments

Sandrine Hugues, PhD
Julie Quinet, PhD
Clara Bourrelly, MS
Patrick Cavanagh, PhD

Human Frontier Science Program
Inserm
ANR
European Research Council
POSITION (P. Cavanagh)