

Justus Liebig Universität
 Dept of Psychology (Prof. Karl Gegenfurtner)
 2018 Oct 31st

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

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Morphological diversity & Functional regularities

Across living animals, several differences are observed in the :

- sensory organs (retina, cochlea, olfactory bulb, etc.),
- motor plants (extra-ocular and neck muscles, geometry etc.)
- neural circuits

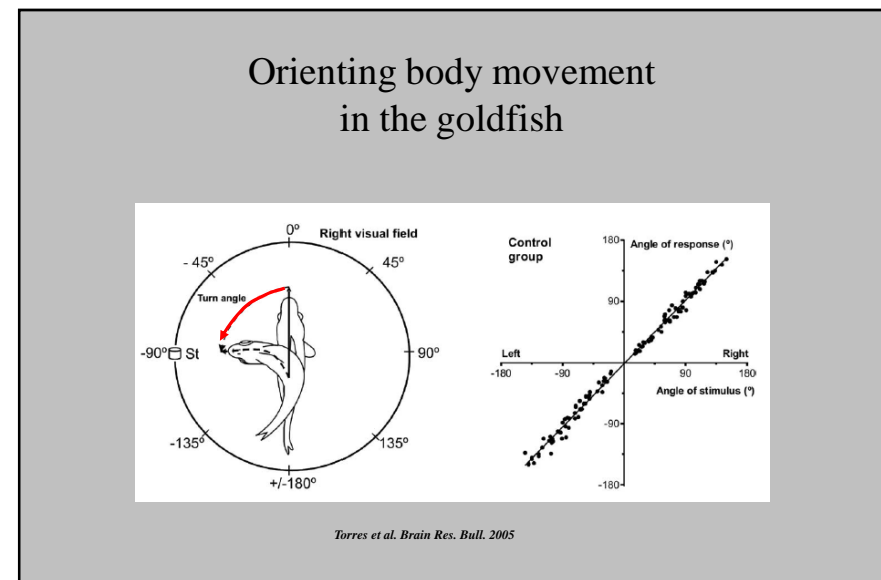
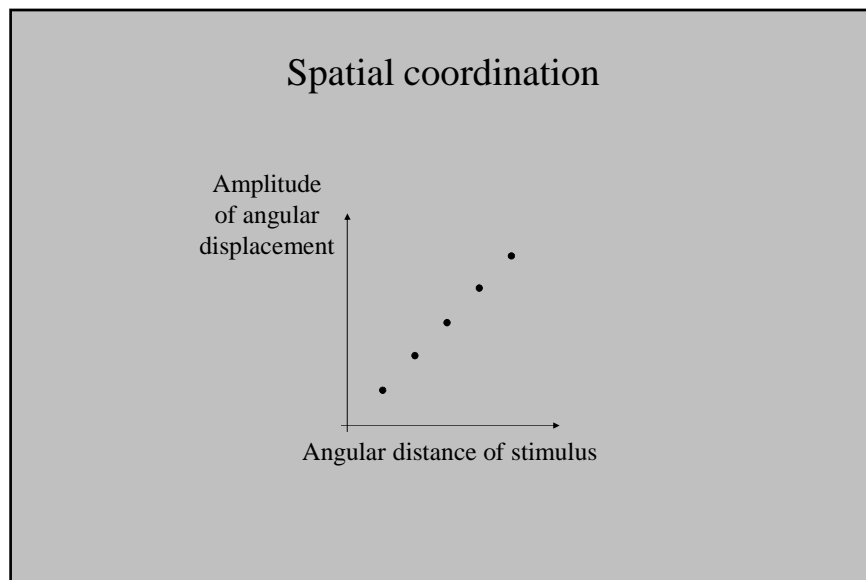
involved in transforming a sensory event into an **orienting response** (OR).

In spite of this morphological diversity, some **regularities** are found :

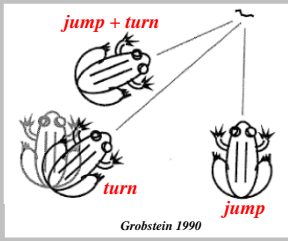
- between individuals within a given family
- between families within a given species
- between species

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

Spatial regularity : its metrical properties (amplitude and direction) fit with the extent of the environment with a variability which is relatively delimited.



Orienting body movement in the frog



orient the gaze toward the target
→
change in (visuomotor) interaction field

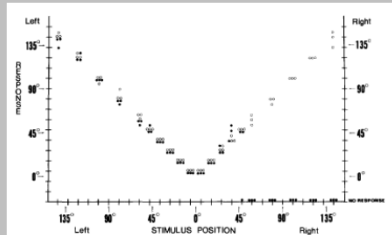


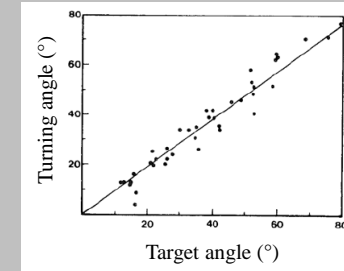
Fig. 1. Orienting behavior of a frog before and after section of the right optic nerve. Stimulus positions are shown by the short lines on the horizontal axis and are defined as number of degrees to the right or left around the animal from the snout. Response angles are shown on the vertical axis. Stimuli 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

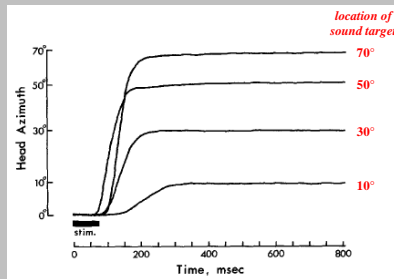


Schülert & Dicke J. Exp Biol 2002



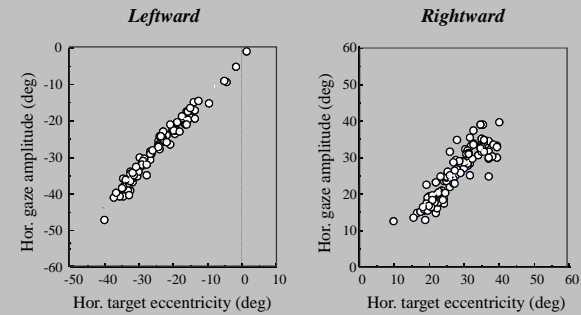
Werner & Himstedt
Zool. Jb. Physiol. 1985

Orienting head movement in the barn owl



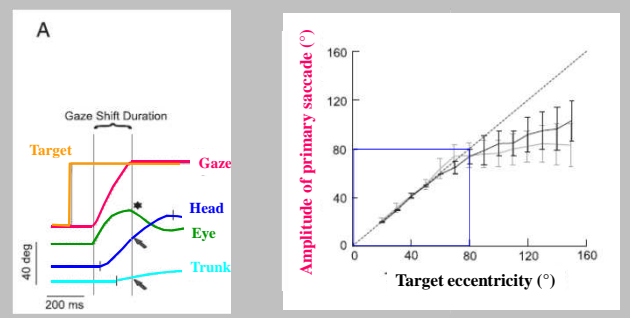
Knuudsen, Blasdel & Konishi JCP 1979

Orienting gaze shift in the cat (head free)



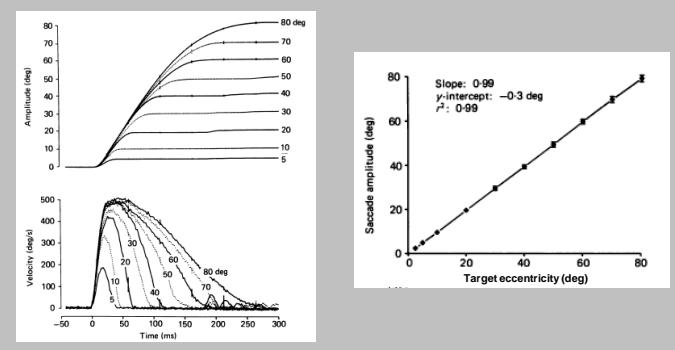
modified from Goffart & Pélisson JNP 1994

Orienting gaze shift in the monkey (head free)



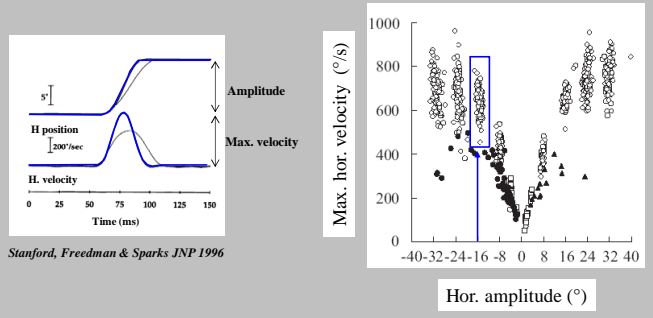
McCluskey & Cullen JNP 2007

Eye saccades in the human subject



Collewijn et al JP 1988

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



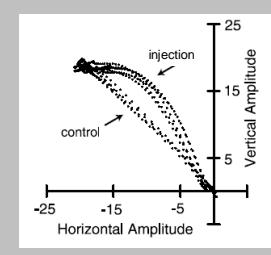
Stanford, Freedman & Sparks JNP 1996

Quinet & Goffart JNP 2009

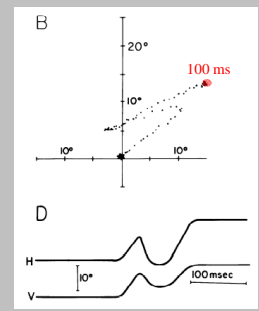
Robustness : spatial accuracy is maintained even after experimental perturbations

Pharmacological inactivation (Pontine Reticular Formation)

Brief electrical microstimulation (deep Superior Colliculus)



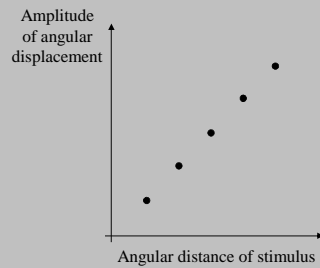
Barton, Nelson, Gandhi & Sparks JNP 2003



Sparks & Mays JNP 1983

Robust relation

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

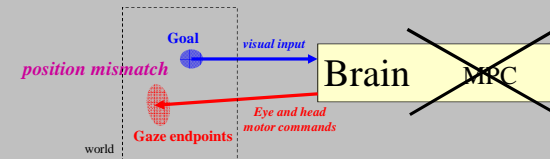


What are the (neuro) biological foundations of this relationship ?

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

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



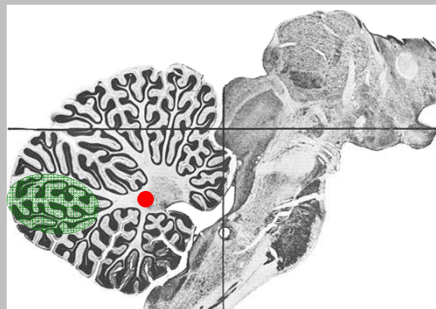
The medio-posterior cerebellum

Lobules VIc-VII

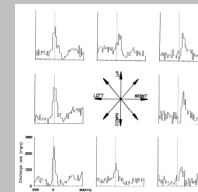


caudal Fastigial Nuclei
(Fastigial Oculomotor Regions)

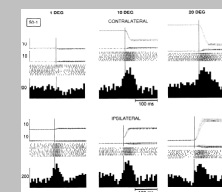
- Saccade-related activity*
- Pursuit-related activity*
- Vergence-related activity*



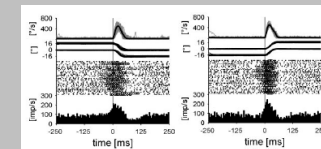
Saccade-related neurons in the caudal fastigial nucleus (head-restrained monkey)



Ohtsuka & Noda JNP 1991



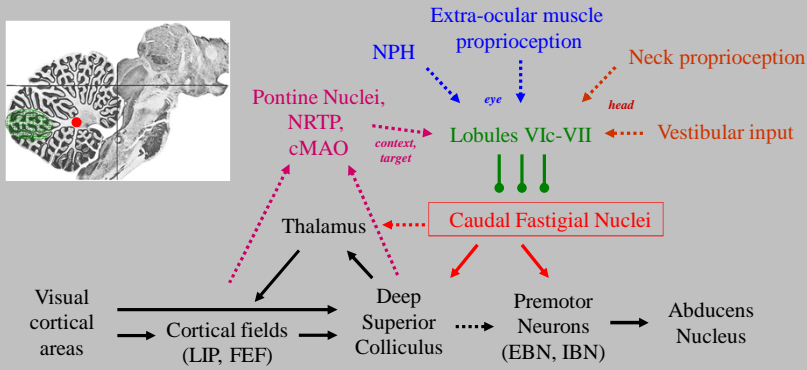
Fuchs, Robinson & Straube JNP 1993



Kleine, Guan & Büttner JNP 2003

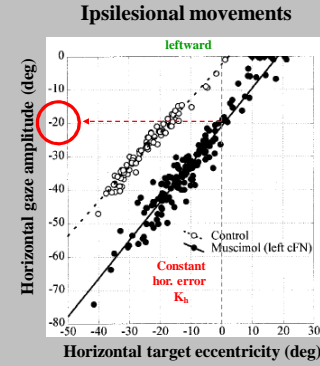
1. Burst of action potentials for all saccades regardless of amplitude and direction
2. Sustained discharge during inter-saccadic intervals

The medio-posterior cerebellum



Gaze dysmetria

Head-FREE cat

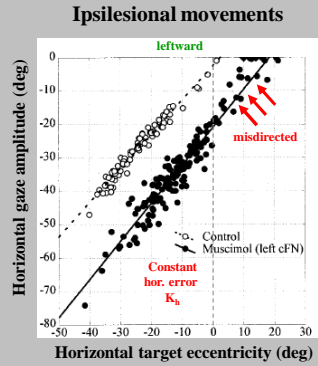


~20 deg !!!

modified from Goffart & Pélisson JNP 1998

Gaze dysmetria

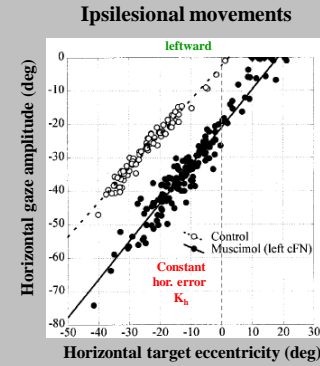
Head-FREE cat



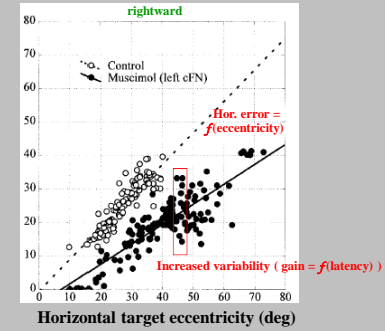
modified from Goffart & Pélisson JNP 1998

Gaze dysmetria

Head-FREE cat

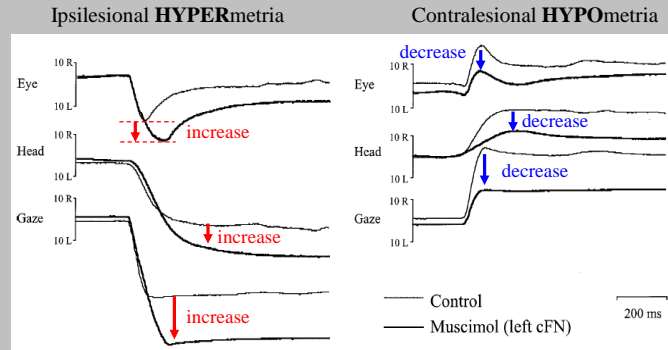


Contralateral movements



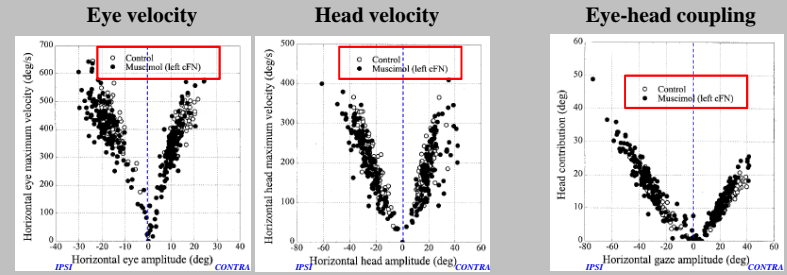
modified from Goffart & Pélisson JNP 1998
(see also Goffart & Pélisson JPhysiol 1997)

Dysmetria affects eye and head movements



modified from Goffart, Pélisson & Guillaume JNP 1998

No sign of movement execution disorder



modified from Goffart, Pélisson & Guillaume JNP 1998

Control (pre-injection)

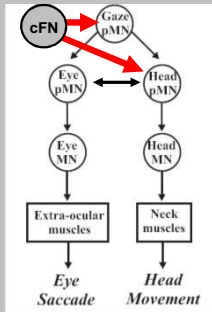


Deficit in head orientation

Muscimol (right cFN)



Cat

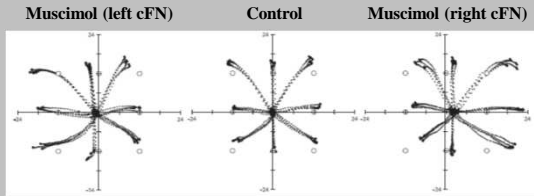


- Gaze dysmetria due to dysmetric **eye + head**
- Eye/head velocity **unchanged**
- Eye/head coupling **unchanged**

Goffart & Pétilson JP London 1997
 Goffart & Pétilson 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



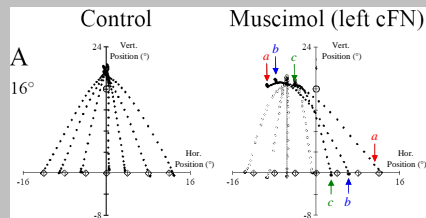
Goffart, Chen & Sparks JNP 2004

Ipsilesional saccades : **horizontal** component is **hypermetric**

Contralateral saccades : **horizontal** component is **hypometric**

Horizontal error is not constant

unlike the head-free cat

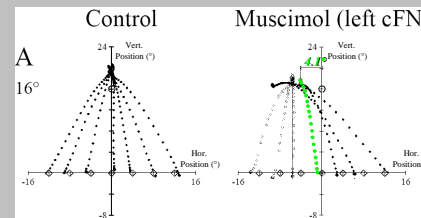


modified from Goffart, Chen & Sparks JNP 2004

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

Horizontal error is not constant

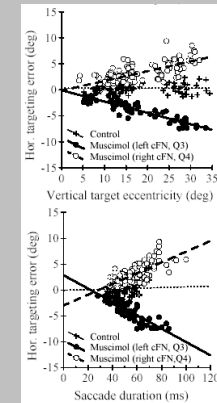
unlike the head-free cat



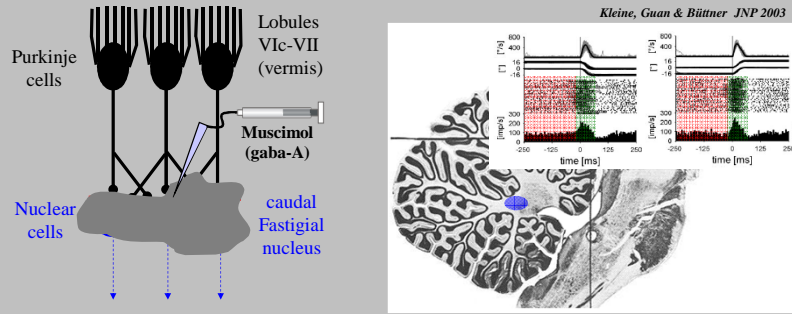
modified from Goffart, Chen & Sparks JNP 2004

Hor. error. = $f(\text{target eccentricity})$
 $f(\text{saccade duration})$

Vertical saccades

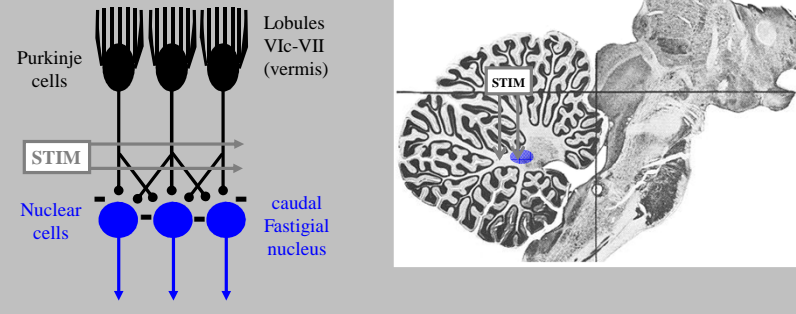


Impairment of **planning** or **execution** ?



Duration of inactivation ~ 2-3 hours :
 Long-lasting perturbation does not allow distinction **pre-saccadic** versus **intra-saccadic** deficits

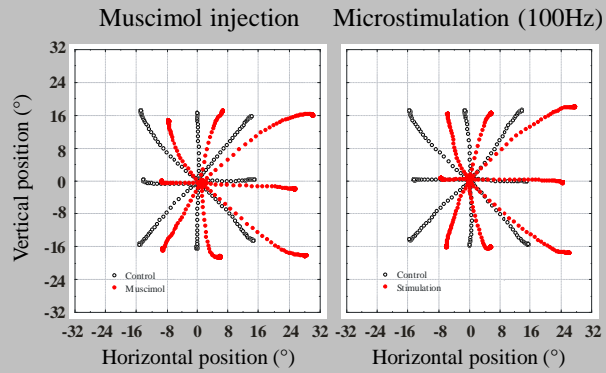
Inhibition of cFN activity with electrical microstimulation



Purkinje cells inhibit cFN neurons with Gaba-A as a neurotransmitter.
 By stimulating their axons, one should be able to mimic the effects of muscimol.

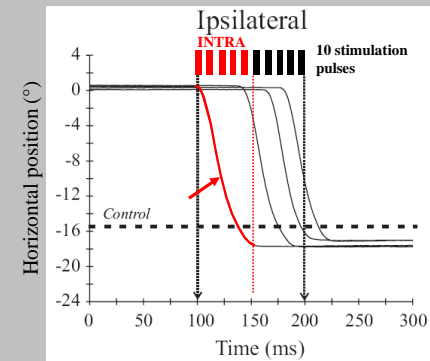
Inhibition of cFN

Right cFN (rebound saccades removed)



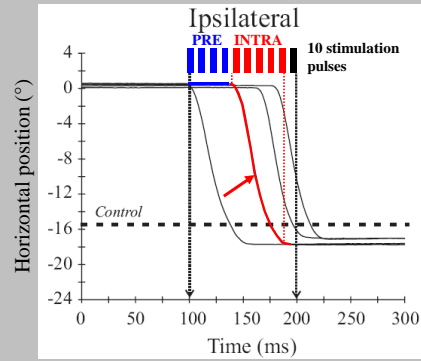
Time window of the perturbation

left caudal Fastigial Nucleus



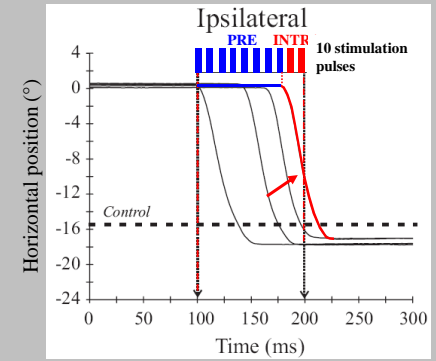
Time window of the perturbation

left caudal Fastigial Nucleus



Time window of the perturbation

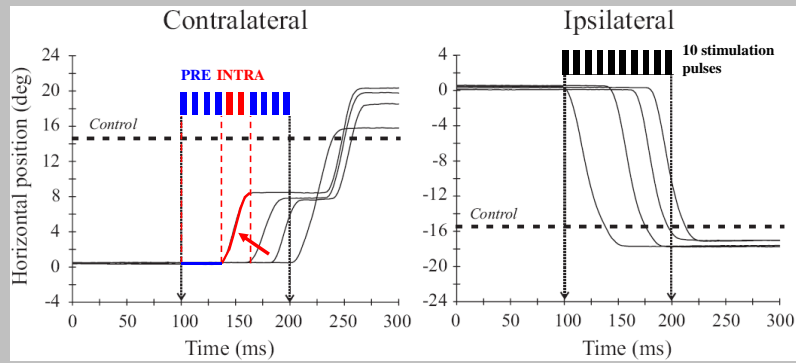
left caudal Fastigial Nucleus



Increasing the number of pre-saccadic pulses does not change the magnitude of hypermetria

Time window of the perturbation

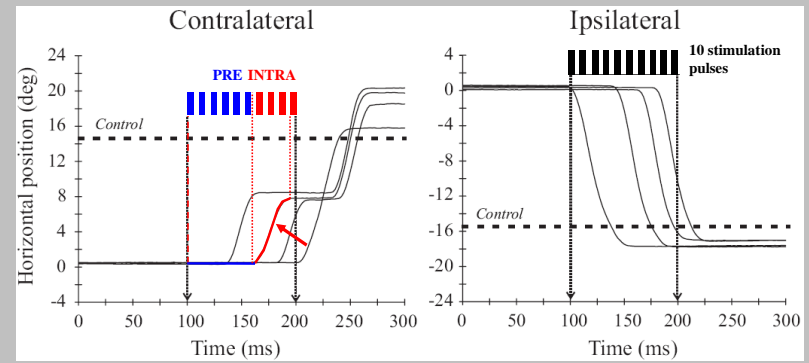
left caudal Fastigial Nucleus



Goffart & Quinet in preparation

Time window of the perturbation

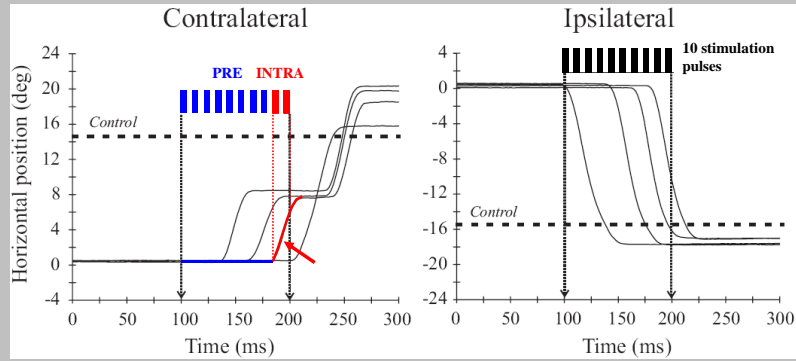
left caudal Fastigial Nucleus



Goffart & Quinet in preparation

Time window of the perturbation

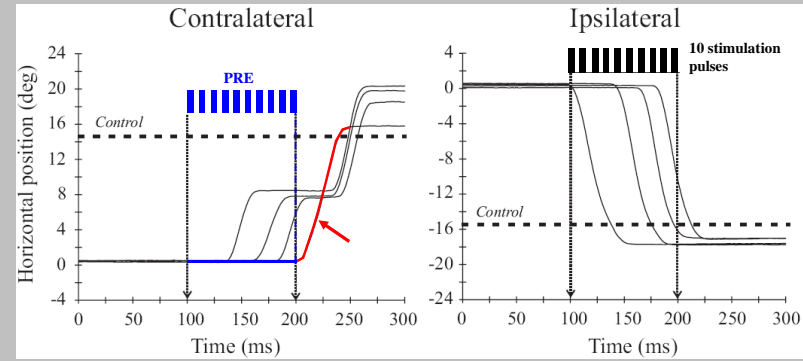
left caudal Fastigial Nucleus



Goffart & Quinet in preparation

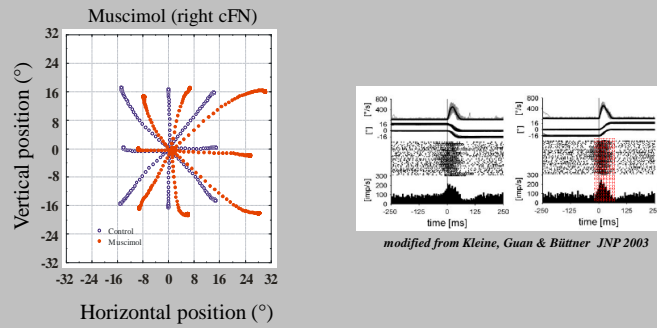
Time window of the perturbation

left caudal Fastigial Nucleus



Goffart & Quinet in preparation

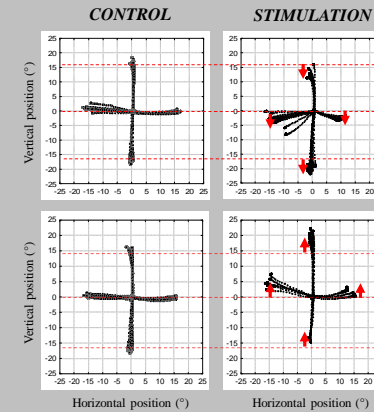
Dysmetria of the **horizontal** component due to unilateral suppression of intrasaccadic spikes



modified from Kleine, Guan & Büttner JNP 2003

Dysmetria of the **vertical** component following a perturbation **outside** the FOR

following a perturbation **outside** the FOR

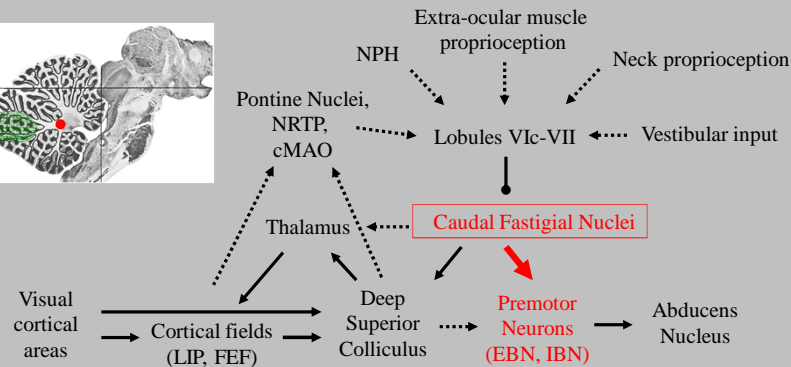
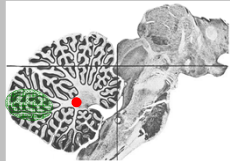


One day, site Y

Next day, same site Y

Goffart et al. unpublished observations

Fastigio-reticular projections and the control of horizontal saccade amplitude

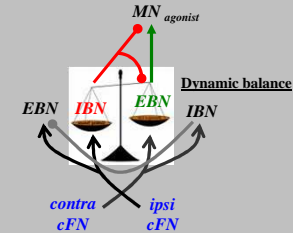


Bilateral hypothesis

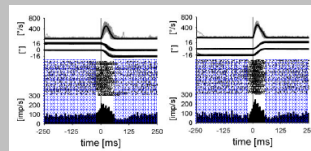
J Neurophysiol 92: 3351-3367, 2004.
First published June 30, 2004; doi:10.1152/jn.01199.2003.

Deficits in Saccades and Fixation During Muscimol Inactivation of the Caudal Fastigial Nucleus in the Rhesus Monkey

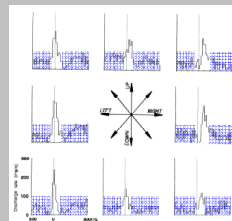
For every saccade (horizontal, oblique or vertical), the **left and right cFN** regulate the **balance** of activity between **excitatory** input (EBNs) and **inhibitory** input (IBNs) to the motor and internuclear neurons in the abducens nucleus (Goffart, Chen & Sparks *J Neurophysiol* 2004).



Does sustained cFN activity have any oculomotor expression?



Kleine, Guan & Büttner *JNP* 2003

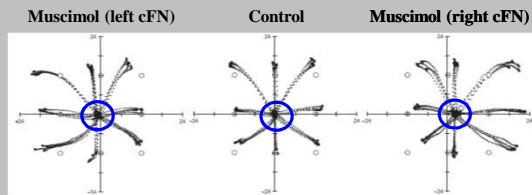


Ohtsuka & Noda *JNP* 1991

Ipsilesional fixation offset

like in the head-free cat

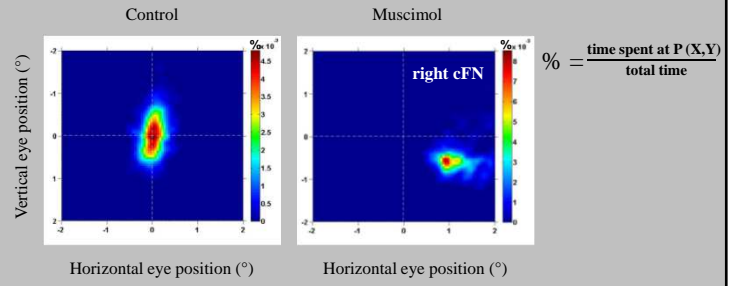
target LEDs @ 145 cm : 0.25° visual angle, mesopic conditions



Goffart, Chen & Sparks *JNP* 2004

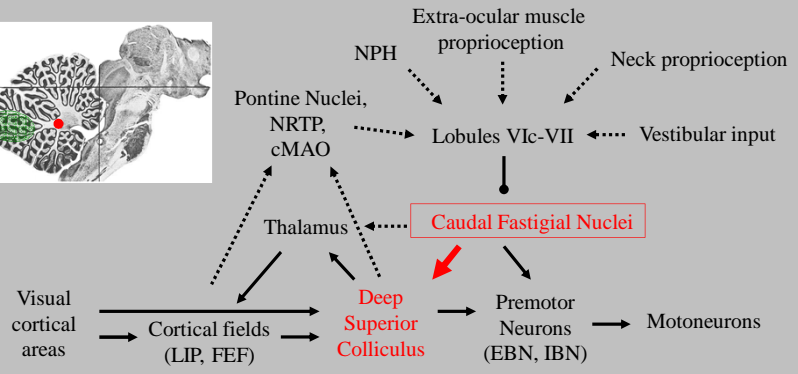
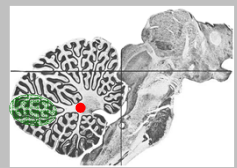
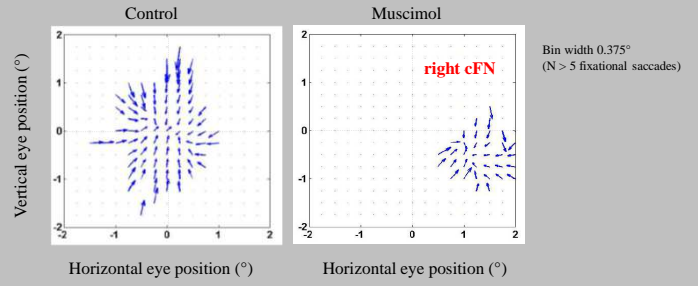
Fixation offset : shift in the scatter of eye positions during fixation

Fixation offset : dwelling time



Directional field of fixational saccades

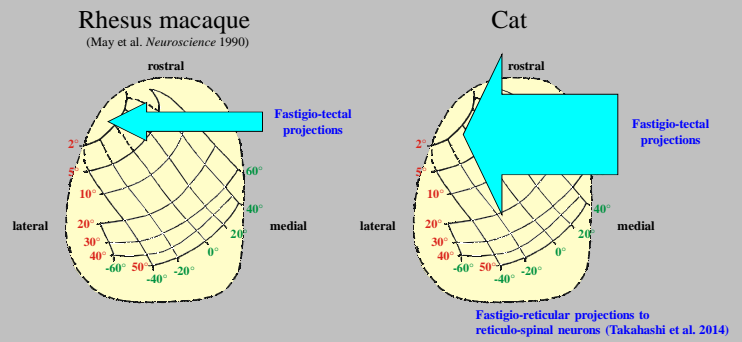
like in the head-free cat



Comparative neuroanatomy / neurology

In the monkey, a "spatial" deficit similar to that observed in the cat, is observed when we considers the small saccades generated while a visual target is being fixated.

The difference between the feline and primate disorders could result from differences in the extent of fastigio-tectal projections.



Visual Fixation as Equilibrium: Evidence from Superior Colliculus Inactivation

Laurent Goffart,¹ Ziad M. Hafed,² and Richard J. Krauzlis^{1,3}

¹Centre de Neurosciences de la Vision, 13005 Centre National de la Recherche Scientifique, Aix-Marseille Université, 13385 Marseille, France; ²Werner Reichardt Centre for Integrative Neuroscience, 72076 Tübingen, Germany; ³Systems Neurobiology Laboratory, Salk Institute for Biological Studies, La Jolla, California 92037; and ⁴Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, Maryland 20892

Journal of Neuroscience 2012

Equilibrium requires symmetry:
The symmetry is achieved by modulations exerted by projections from the cFN to the brainstem

Experimental prediction

Equilibrium requires symmetry:
The symmetry is achieved by modulations exerted by projections from the cFN to the brainstem

Fixation offset after muscimol injection in the rostral SC

POSITION

Ipsilesional fixation offset
Saccades to peripheral targets are accurate

AMPLITUDE

No asymmetry in the H or V amplitude of fixational saccades

Goffart, Hafed & Krauzlis JN 2012

Asymmetry in the hor. ampl. of fixational saccades after cFN inactivation

HORIZONTAL

VERTICAL

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

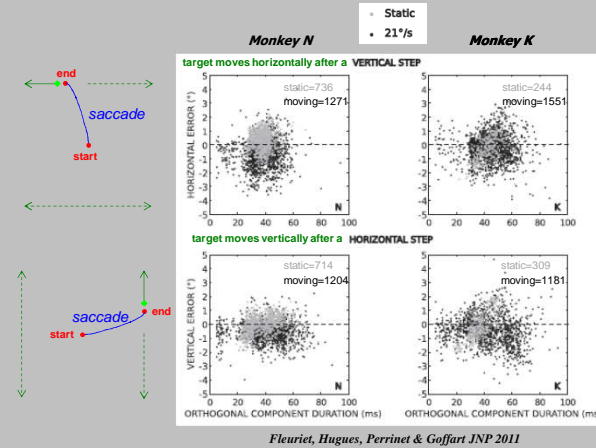
Lorenzo Guerrasio,¹ Julie Quinet,² Ulrich Bättner,¹ and Laurent Goffart³

Predictive chronometric control

"... in programming interceptive saccades, 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 "...
 "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)

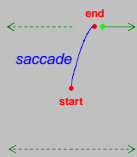
Accuracy and precision of saccades



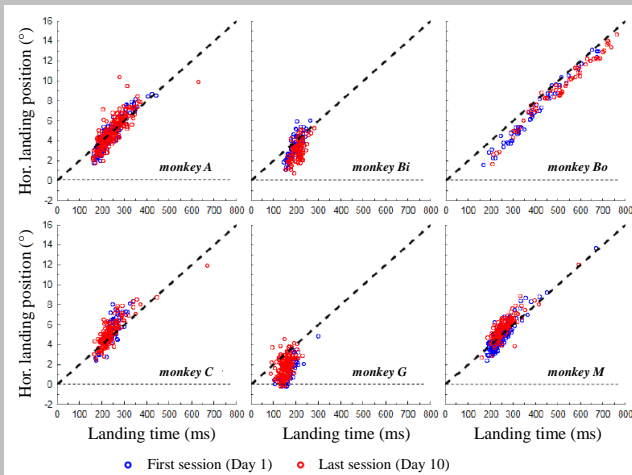
Comparable errors between saccades toward a **static** versus **moving** target

No evidence for a spatial lead of saccade endpoints

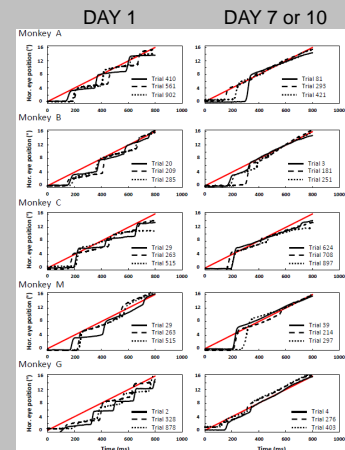
No spatial lead of endpoints after practice



Constant speed = 20°/s



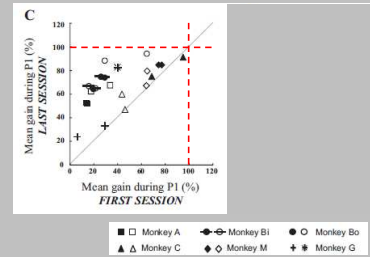
Practice influences post-saccadic pursuit



J Neurophysiol 116:2779-2791, 2016. First published September 28, 2016; doi:10.1152/jn.00191.2016

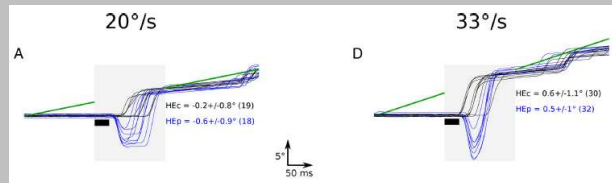
Learning the trajectory of a moving visual target and evolution of its tracking in the monkey

Clara Bourreily,^{1,2} Julie Quinet,¹ Patrick Cavanagh,² and Laurent Goffart¹
¹Institut de Neurosciences de la Timone, CNRS 7309, Centre National de la Recherche Scientifique, Aix-Marseille Université, Marseille, France; and ²Laboratoire Psychologie de la Perception, CNRS 4242, Centre National de la Recherche Scientifique, Université Paris Descartes, Paris, France



No spatial lead after perturbation

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

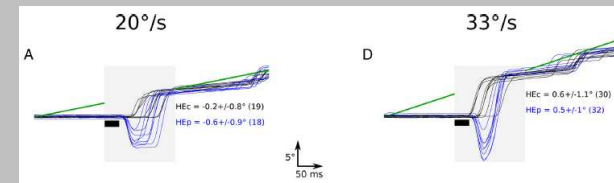


Fleuriot & Goffart JN 2012

"Here-and-now" hypothesis :

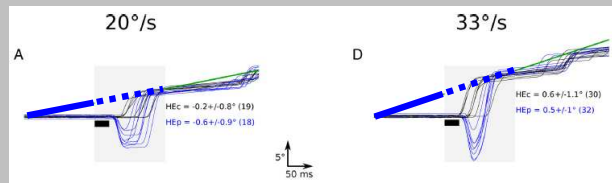
Interceptive saccades precisely capture the target, where it is when it is there

What signals drive the correction ?



Fleuriot & Goffart JN 2012

What signals drive the correction ?



Fleuriot & Goffart JN 2012

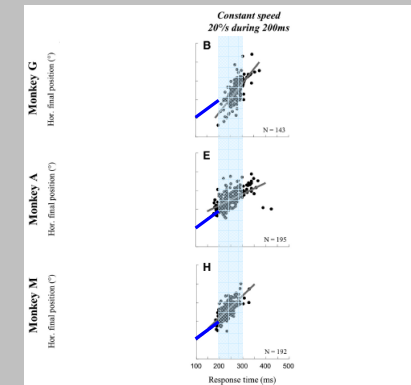
Extrapolation ? → diffusion of residual pre-occlusion signals

11706 • The Journal of Neuroscience, August 26, 2015 • 35(34):11700–11706

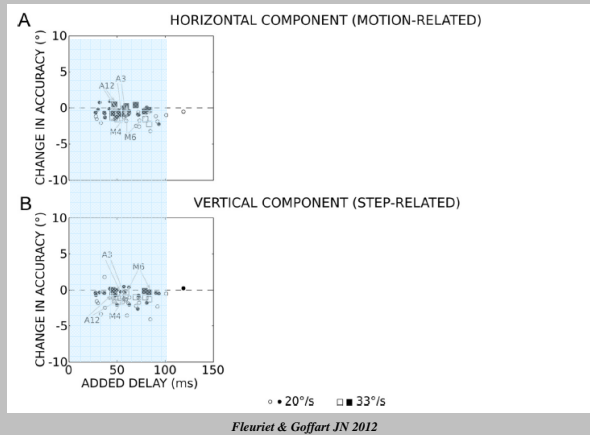
Behavioral/Cognitive

Does the Brain Extrapolate the Position of a Transient Moving Target?

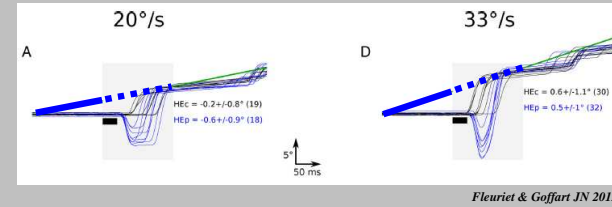
Quinet & Goffart JN 2015



Interception of perturbed saccades delayed by <150 ms

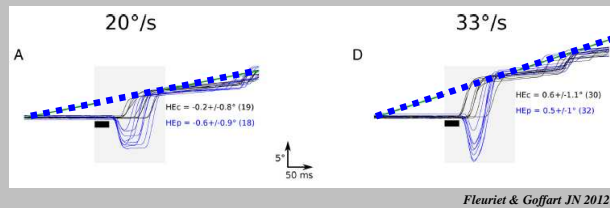


What signals drive the correction ?



Extrapolation ? → diffusion of residual pre-occlusion signals **POSSIBLE**

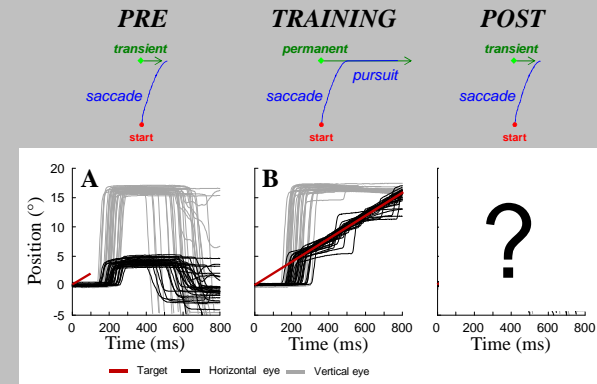
What signals drive the correction ?



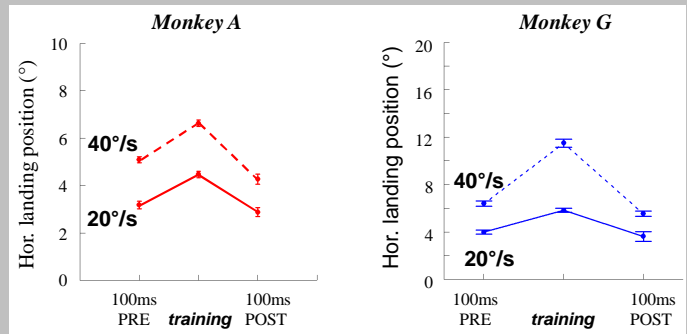
Extrapolation ? → diffusion of residual pre-occlusion signals **POSSIBLE**

A memorized trajectory of target in the peripheral visual field ?

Memorized trajectory ?

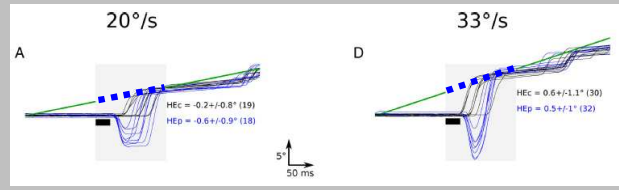


NOT a memorized trajectory



Quinet & Goffart in preparation

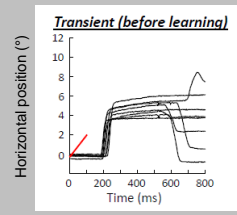
What signals drive the correction ?



Fleuret & Goffart JN 2012

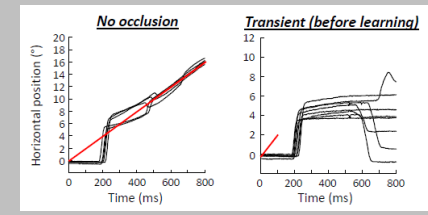
Extrapolation ? → diffusion of residual pre-occlusion signals **POSSIBLE**
 A memorized target trajectory **APPARENTLY NO**
 Interpolation ? → residual signals merging with target expectation?

Filling-in the occlusion



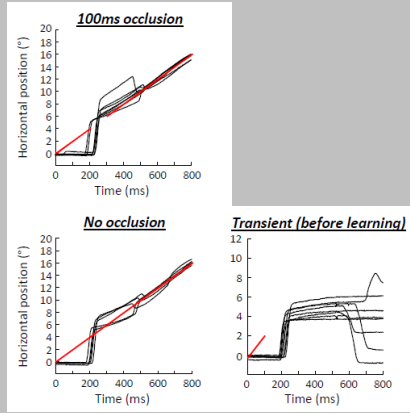
Quinet & Goffart in preparation

Filling-in the occlusion



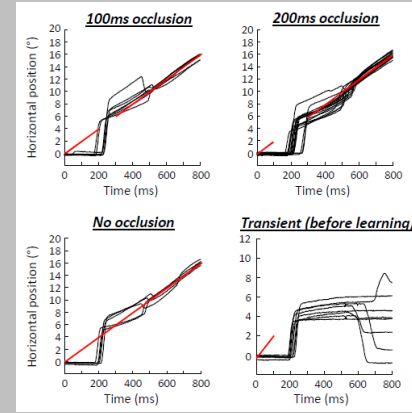
Quinet & Goffart in preparation

Filling-in the occlusion



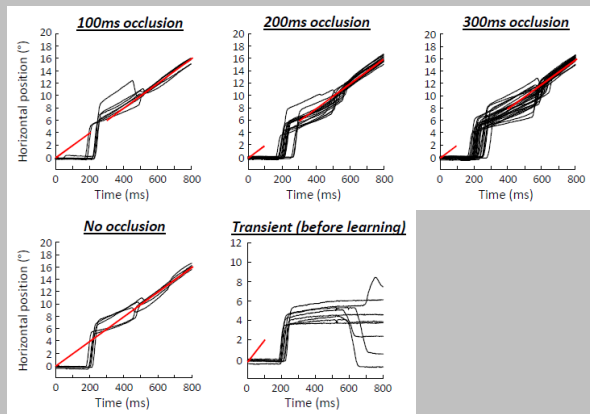
Quinet & Goffart in preparation

Filling-in the occlusion



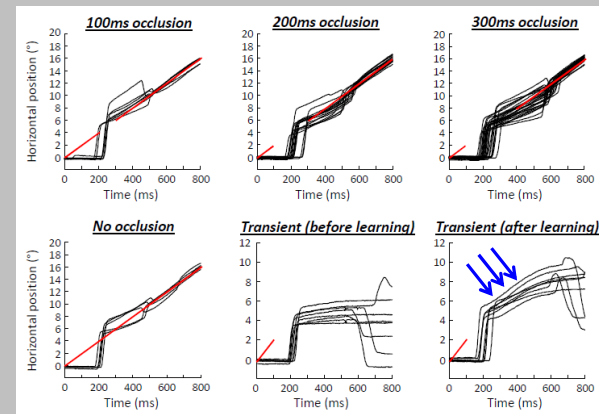
Quinet & Goffart in preparation

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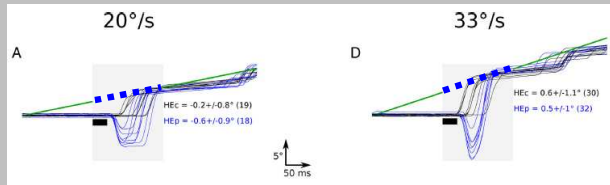
Quinet & Goffart in preparation

Filling-in the occlusion



Quinet & Goffart in preparation

What signals drive the correction ?



Fleuriot & Goffart JN 2012

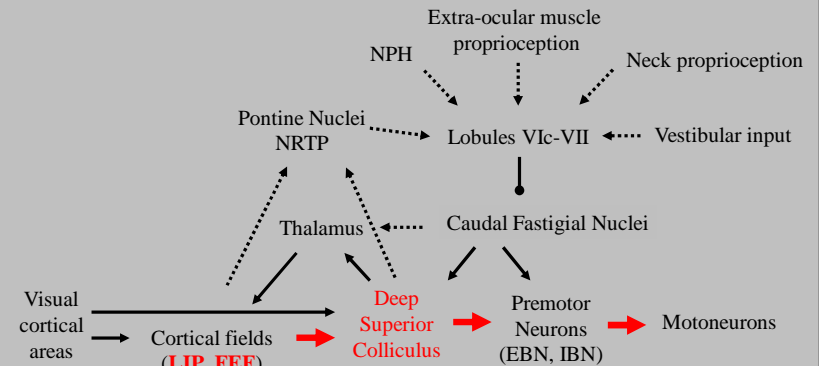
Extrapolation : diffusion of residual pre-occlusion signals **POSSIBLE**

A memorized target trajectory ? **POSSIBLY NOT**

Interpolation ? → residual signals merging with target expectation

→ **Alternative : memorized pursuit eye movement** **POSSIBLE**

Brain control of accurate tracking (interceptive saccade)



J Neurophysiol 104:206-216, 2011

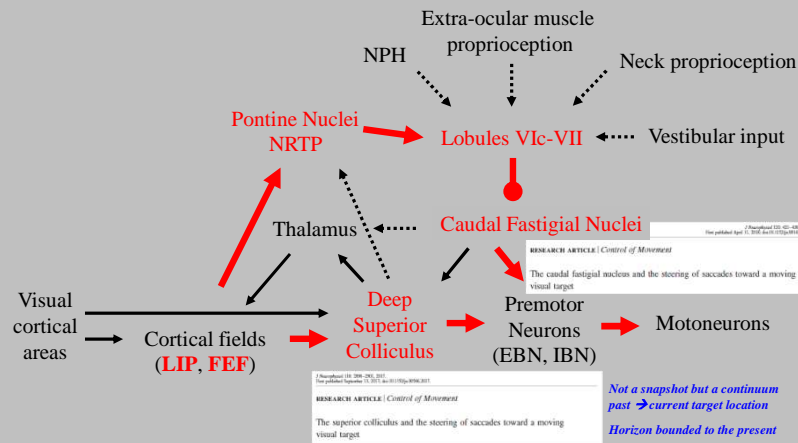
First published April 11, 2010; doi:10.1152/jn.00141.2010

RESEARCH ARTICLE | Control of Movement

The superior colliculus and the steering of saccades toward a moving visual target

Not a snapshot but a continuum past → current target location
Horizon bounded to the present

Brain control of accurate tracking (interceptive saccade)



J Neurophysiol 104:450-459, 2011

First published April 11, 2010; doi:10.1152/jn.00141.2010

RESEARCH ARTICLE | Control of Movement

The caudal fastigial nucleus and the steering of saccades toward a moving visual target

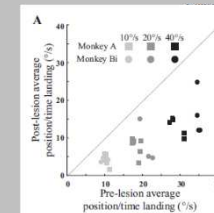
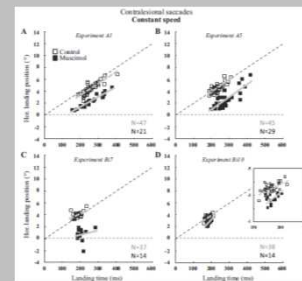
Not a snapshot but a continuum past → current target location
Horizon bounded to the present

Fastigial control of interceptive saccades

J Neurophysiol 120:421-438, 2018.
First published April 11, 2018; doi:10.1152/jn.00141.2018

RESEARCH ARTICLE | Control of Movement

The caudal fastigial nucleus and the steering of saccades toward a moving visual target



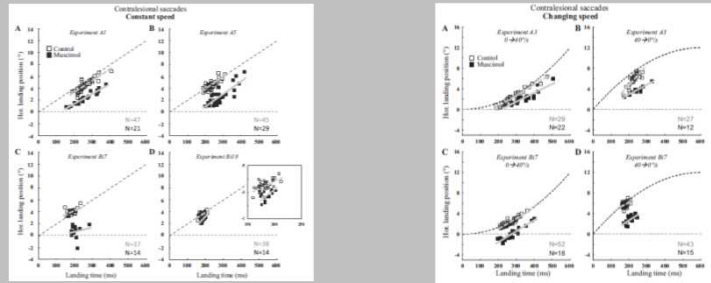
Bourrelly, Quinet & Goffart JNP 2018a

Fastigial control of interceptive saccades

J Neurophysiol 120: 421–438, 2018.
First published April 11, 2018; doi:10.1152/jn.00141.2018.

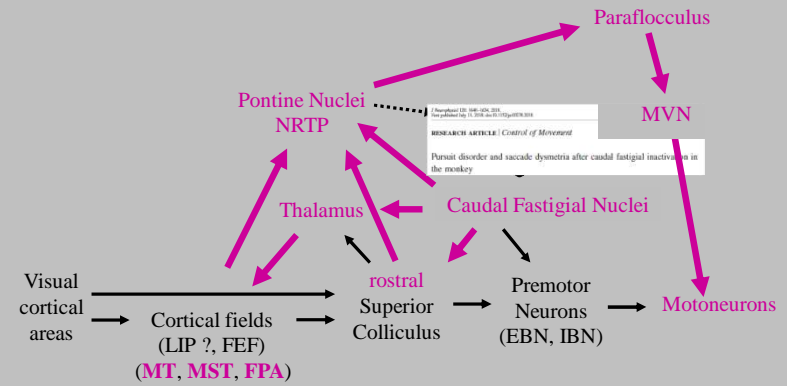
RESEARCH ARTICLE | *Control of Movement*

The caudal fastigial nucleus and the steering of saccades toward a moving visual target



Bourelly, Quinet & Goffart JNP 2018a

Brain control of accurate tracking (smooth pursuit)

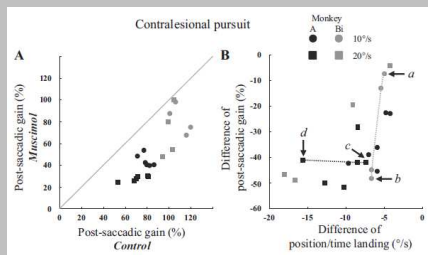


Fastigial control of visual tracking (saccade + pursuit)

J Neurophysiol 120: 1640–1654, 2018.
First published July 11, 2018; doi:10.1152/jn.00278.2018.

RESEARCH ARTICLE | *Control of Movement*

Pursuit disorder and saccade dysmetria after caudal fastigial inactivation in the monkey



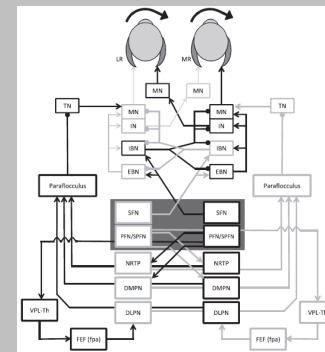
Bourelly, Quinet & Goffart JNP 2018b

Fastigial control of visual tracking (saccade + pursuit)

J Neurophysiol 120: 1640–1654, 2018.
First published July 11, 2018; doi:10.1152/jn.00278.2018.

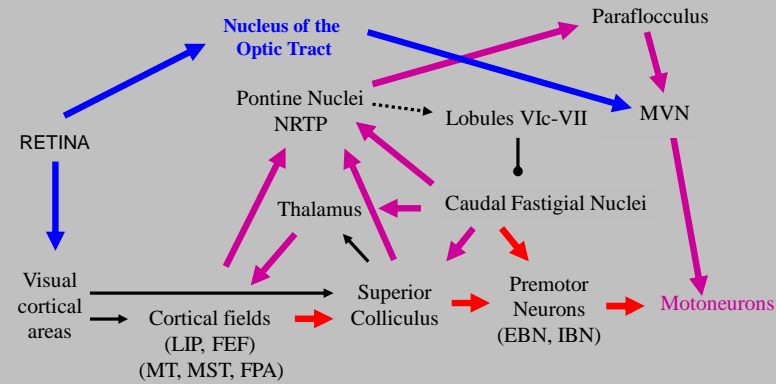
RESEARCH ARTICLE | *Control of Movement*

Pursuit disorder and saccade dysmetria after caudal fastigial inactivation in the monkey



Bourelly, Quinet & Goffart JNP 2018b

Brain control of accurate tracking



Conclusions

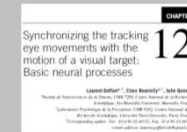
In the trained and untrained monkey, saccades toward a target moving with a constant speed are as accurate as saccades toward a static target. They land close to the target location.

Some studies invoke an "internal model" of the target trajectory.

- What does this notion mean neurophysiologically? What would be its neural representation?
- How is the locality (x,y,z,t) represented in the spatiotemporally distributed brain activity?
- Must we presume a "space-time" manifold within which the neural image of the target would evolve?

Our alternative viewpoint does not posit any recipient but considers local object-related activities.

The ability to foveate a moving target tells us that changes in gaze direction synchronize with target changes. Initially biased by signals related to the past target location, the lag would gradually be reduced through a learning process that would involve a neuronal *synchronization* process.



Progress in Brain Research, vol. 235, 2017

Conclusions

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WORKING HYPOTHESIS :

While post-saccadic pursuit velocity increases, the *size of the active population* increases in fastigio-recipient regions (like DMPN, DLPN, rostral SC, VPL Thalamus).

Likewise for the interceptive saccade, the change in amplitude consists of adjusting *the number of synchronous burst neurons* in the pontomedullary RF.

Acknowledgments



Experiments in the caudal Fastigial Nucleus

Head-free cat

Denis Pélisson
Alain Guillaume

Head-restrained and -unrestrained monkey

David L. Sparks
Longtang L. Chen

Lorenzo Guerrasio
Ulrich Büttner

Julie Quinet
Clara Bourrelly
Patrick Cavanagh

Experiments in the deep Superior Colliculus (monkey)

Ziad M. Hafed
Richard J. Krauzlis

Aaron L. Cecala
Neeraj J. Gandhi

Behavioral experiments

Sandrine Hugues

Human Frontier Science Program



Inserm
Institut national de la santé et de la recherche médicale

ANR
Agence Nationale de la Recherche



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