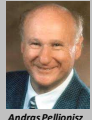


Seminar at Institut de Neurosciences des Systèmes
 invited by Pr. Marcel CARRERE
 Marseille, 2003 October 19th


Critique of the neuronal encodings of movement kinematics and number

Laurent Goffart
laurent.goffart@cns.fr



**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.



Neuroscience 1982

Space-time: dogma and redefinition

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.

Espace-temps: dogme et redéfinition

La compréhension de la fonction cérébrale est souvent limitée par l'acceptation tacite de concepts connus pour être fondamentalement inappropriés. Un exemple est le principe selon lequel le cerveau, dans son fonctionnement interne, utilise des cadres de référence spatio-temporels similaires à ceux utilisés en mécanique classique.

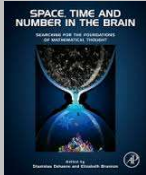
Cependant, l'utilisation de systèmes de coordonnées distincts pour l'espace et le temps dépend du concept de simultanéité. Puisque dans le cerveau il n'existe pas d'agent de simultanéité "instantanée" comparable à la lumière, l'utilisation classique de coordonnées spatiales et temporelles séparées est inapplicable dans le cas de la description du fonctionnement interne du SNC.

Confusions

Over the past decades, confusions were made in the domain of cognitive neuroscience between

- the concepts
- the measurements (measured values and subsequent numerical transformations) and
- the physiological processes that generate the measured phenomenon.

Theoretical notions associated with some measurements led some authors to imagine options such as a "coding" in the brain of space, time, number, movement duration, speed, acceleration, Geometry and Arithmetic.



2011

Encoding of movement time by populations of cerebellar Purkinje cells

Peter Tiber, Peter W. Bink, Roman Bauer & Dasha Sussner

2000

letters to nature

AN ENHANCED ARGUMENT FOR INNATE ELEMENTARY GEOMETRIC KNOWLEDGE AND ITS PHILOSOPHICAL IMPLICATIONS

HELEN DE CRUZ
 Centre for Logic and Analytical Philosophy

2007

Arithmetic and the brain

Stanislas Dehaene, Nicolas Molko, Laurent Cohen and Anna J Wilson

2004

Current Opinion in Neurobiology 2004, 14:218-224

Use of eye movements to probe "space, time and number in the brain"

Compression of visual space before saccades

John Ross¹, M. Concetta Morrone¹ & David C. Burr^{1,2}

Nature 1997

Saccades compress space, time and number

David C. Burr^{1,2,3}, John Ross³, Paola Binda^{4,5} and M. Concetta Morrone^{6,7}

Trends in Cognitive Sciences 2010

Recruitment of an Area Involved in Eye Movements During Mental Arithmetic

André Knops^{1,2,3*}, Bertrand Thirion^{2,4}, Edward M. Hubbard^{1,2,3}, Vincent Michel^{2,3,4}, Stanislas Dehaene^{1,2,3,5}

Science 2009

Saccadic eye movements cause compression of time as well as space

M Concetta Morrone¹, John Ross² & David Burr^{3,4}

Nature Neuroscience 2005

Correspondences

Eye position predicts what number you have in mind

Tobias Loetscher^{1,2}, Christopher J. Bockisch^{3,3}, Michael E.R. Nicholls¹ and Peter Brugger⁴

Current Biology 2010

Confusions

Over the past decades, confusions were made in the domain of cognitive neuroscience between

- the concepts
- the measurements (measured values and subsequent numerical transformations) and
- the physiological processes that generate the measured phenomenon.

Theoretical notions associated with some measurements led some authors to imagine options such as a "coding" in the brain of space, time, numbers, movement duration, speed, acceleration, Geometry and Arithmetic.

In the neuroscientific study of movement generation, kinematic parameters were imagined to be "encoded" in the activity of neurons. While they emit spikes, the neurons would "speak a coded language" translatable with notions of classical mechanics.

Yet, the movement of the eyeballs is the measurement of their physical change in orientation/position, which is caused by changes in the contraction of extra-ocular muscles, which in turn are the outcome of multiple processes occurring in parallel in the brain and converging on the groups of motor neurons.

To the totally ordered set of numerical values (the time series of measured eye positions), a radically different structure is associated : a dynamic structure, firstly **diffluent** then **confluent**, whose elements are *spatially distributed* and whose activities are *temporally exploded*.

Between the optic nerves and the motor nerves

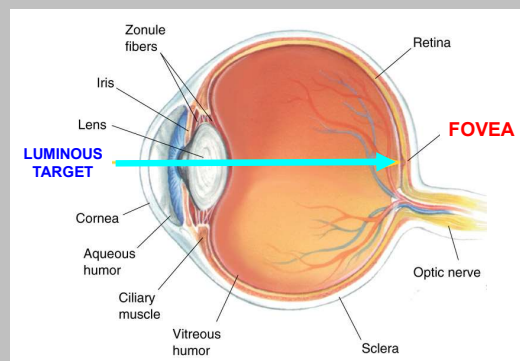
Let's consider the case of a spot of light in the visual field.

At the ends of the **optic nerves**, the retinal excitation triggers flows of activity that manifests in the brain as a kind of tree-like explosion (**difffluence**). The evoked activity propagates spatially. It is distributed in multiple groups of neurons whose activities are more or less persistent.

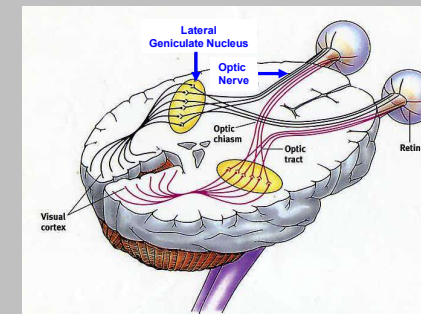
As the activity spreads and joins the groups of cells at the origin of the **motor nerves** innervating the muscles, this explosion is transformed into a kind of compression (**confluence**), of which only the duration matters (longer muscle contractions make *longer* movement) in addition to the recruitment of new groups of neurons and muscles (e.g. extraocular + neck muscles make *larger* movement).

The eye

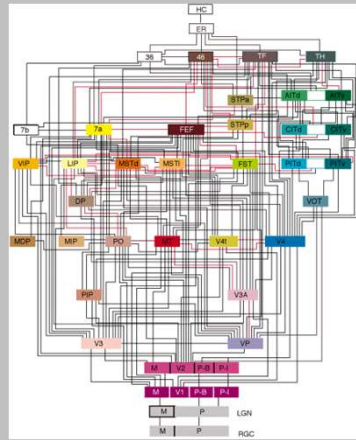
Sagittal view



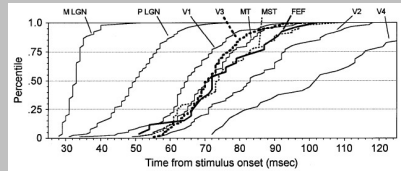
At the end of the optic nerves



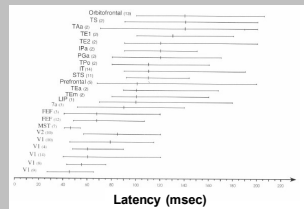
Explosion of visual signals:
spatial and temporal diffuence



Felleman & Van Essen *Cerebral Cortex* 1991

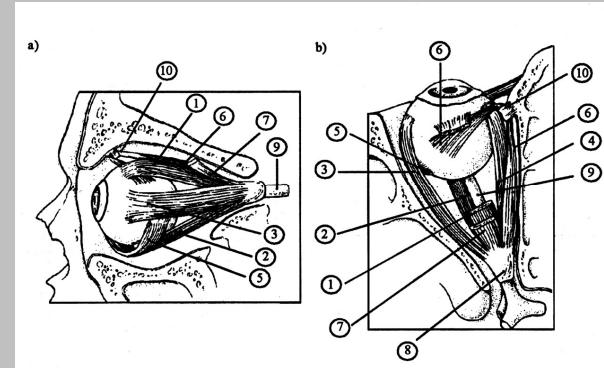


Schmolesky et al. *Journal of Neurophysiology* 1998

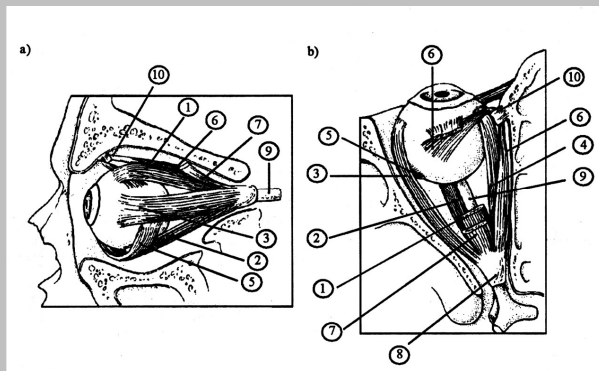


Nowak & Bullier *Cerebral cortex: extrastriate cortex in primates* 1997

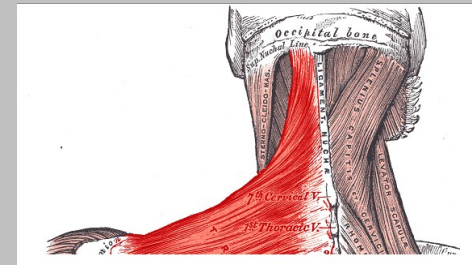
The eye is not only a retina



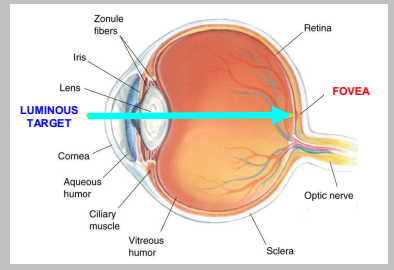
Projection of the target on the fovea
IF & only IF proper contraction of extraocular muscles
(direction of gaze)



Projection of the target on the fovea
IF & only IF proper contraction of neck muscles
(head direction)



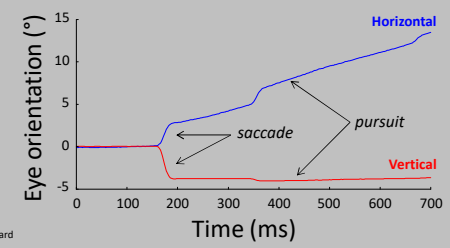
LOOKING AT A TARGET =
contracting several muscles



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

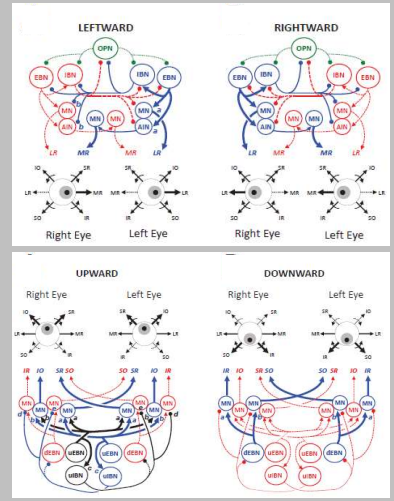
rapid : saccade
slow : pursuit

same muscles and motor nuclei BUT largely distinct central circuits

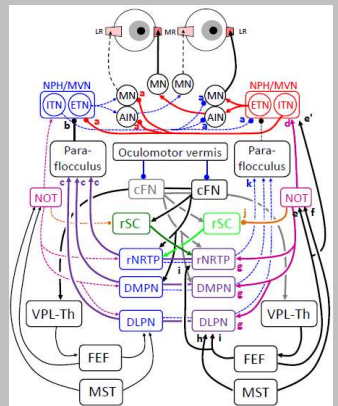


values > 0 : rightward / upward
value = 0 : straight ahead
values < 0 : leftward / downward

SACCADE PREMOTOR NETWORK



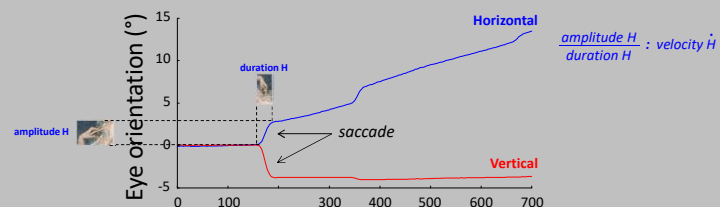
SLOW PURSUIT NETWORK (Horizontal)



Goffart, Quinet & Bourrelly Encyclopedia Human Brain in revision

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

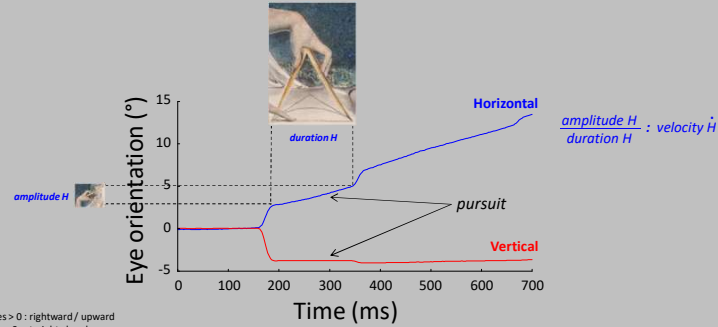
rapid : saccade



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

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

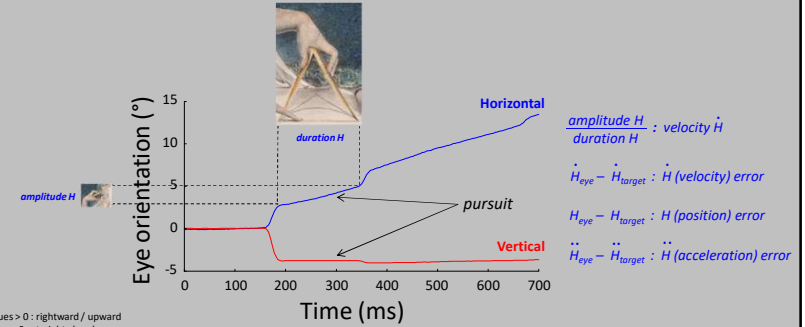
rapid : saccade
slow : pursuit



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

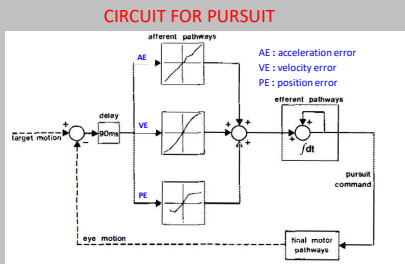
Two types of eye movement in response to the motion of a visual target

rapid : saccade
slow : pursuit

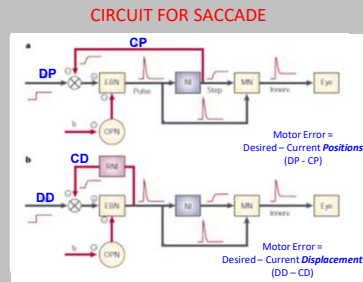


values > 0 : rightward / upward
value = 0 : straight ahead
values < 0 : leftward / downward

Arithmetic and physical quantities "encoded" in the brain activity ?



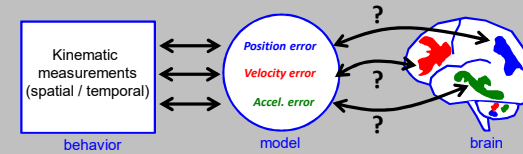
Lisberger, Morris & Tychsen *Annual Rev Neurosci* 1987



Sparks *Nat Neurosci Rev* 2002

Arithmetic and physical quantities "encoded" in the brain activity ?

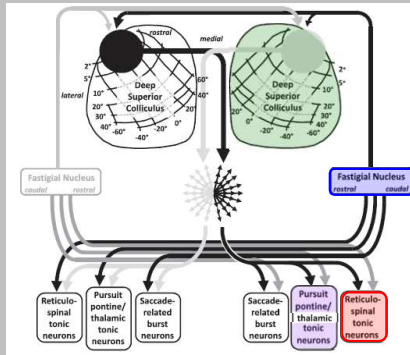
QUESTIONING THE BRAIN-MODEL ISOMORPHISM



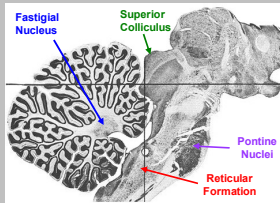
Measuring and modelling the movement of the eyeball (a rigid body) with kinematic notions **does not imply** equivalence in the brain, and notably that the firing of neurons ought to "encode" (*i.e.*, **emit signals related to**) amplitude, velocity or acceleration of the eye movement.

Is an alternative possible ? Does thinking otherwise leads to a dead end ?

Alternative theory



No movement = poly-equilibrium



Journal of Neurophysiology 120: 3234-3245, 2018
 Kinematics and the neurophysiological study of visually-guided eye movements
 Progress in Brain Research, vol. 249, 375-384, 2019

Head orientation as an equilibrium



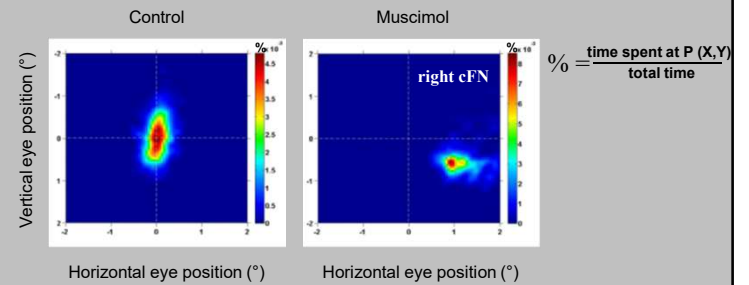
Head orientation as an equilibrium

Impaired after unilateral inactivation of caudal fastigial nucleus



Eye orientation as an equilibrium

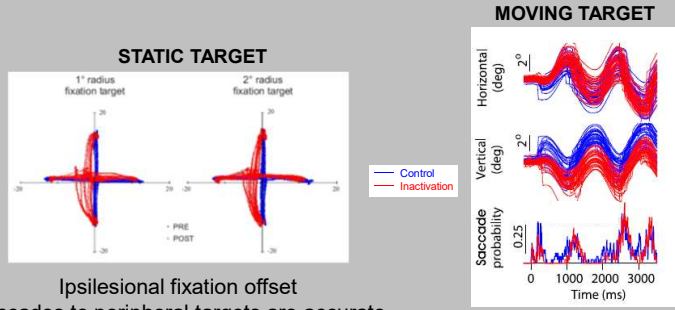
Impaired after unilateral inactivation of caudal fastigial nucleus in the Rhesus monkey



Guerrasio, Quinet et al. Journal of Neurophysiology 2010

Eye orientation as an equilibrium

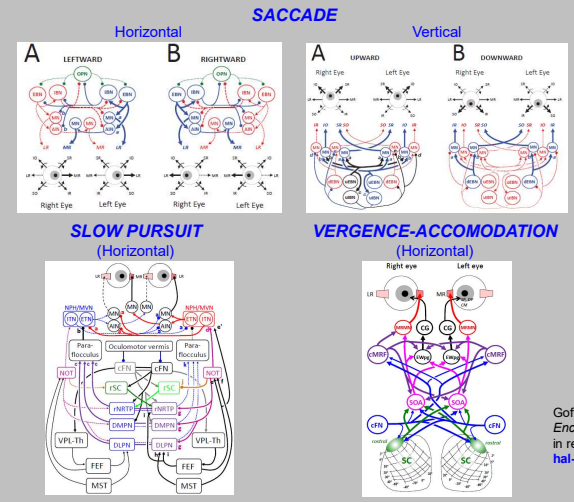
Impaired after unilateral inactivation of *rostral superior colliculus* in the Rhesus monkey



Ipsilesional fixation offset
Saccades to peripheral targets are accurate

Hafed, Goffart & Krauzlis *Journal of Neuroscience* 2008
Goffart, Hafed & Krauzlis *Journal of Neuroscience* 2012

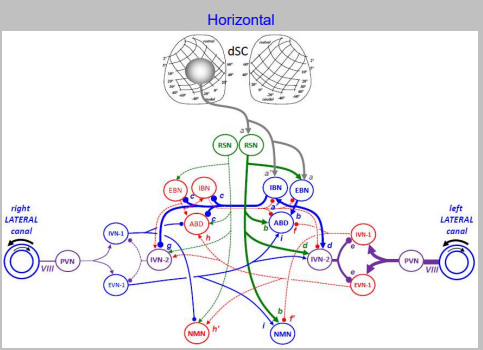
Poly-equilibrium within bilateral networks



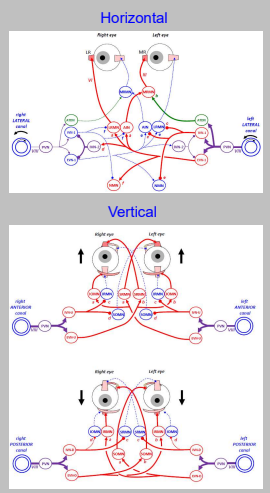
Goffart, Quinet & Bourrelly
Encyclopedia of the Human Brain in revision
hal-03541980

Poly-equilibrium within bilateral networks

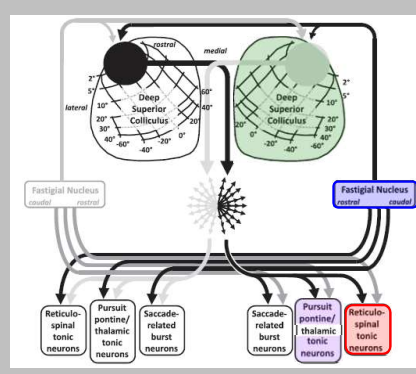
COMBINED EYE-HEAD MOVEMENTS



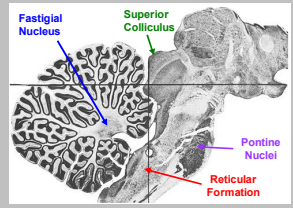
Goffart, Quinet & Bourrelly
Encyclopedia of the Human Brain in revision
hal-03541980



Alternative theory



No movement = poly-equilibrium
→ Movement = restoration of equilibrium



Journal of Neurophysiology 120: 3234-3245, 2018
Kinematics and the neurophysiological study of visually-guided eye movements
Progress in Brain Research, vol. 249, 375-384, 2019

Brain and Mathematics

Alain Berthoz (2005):

Mathematics is "the expression of laws and mechanisms which are in operation in the brain" ...
"a language of the brain on the brain itself, that is to say, since the brain is part of the physical world, [a language] about the Universe and its laws"

Jean-Pierre Changeux (1989):

"Mathematics is in the mathematician's brain, especially in his long-term memory."

Stanislas Dehaene (2010):

"Numbers, like all mathematical objects, are mental constructions whose roots lie ... in the adaptation of the human brain to the regularities of the universe."

Stanislas Dehaene (2012):

"All human brains receive in sharing, from birth, sophisticated mental representations, independent of language that can be described as "proto-mathematical". During its evolution, our brain has been endowed with elementary representations of space, time and number, which we share with many other animal species, and which are the basis of our mathematical intuitions."

Evolutionary epistemology

Franz Wuketits (1984):

"Through the process of adaptation living systems accumulate more and more information about their environment and, thus, represent the structure of the environment they live in; the better the representation of the environment, the better the chance of survival".

There is an "isomorphic relation of patterns of nature to patterns of cognition."

Konrad Lorenz (1941):

"Regarded as a working hypothesis or as a functional organ, the form of thought of numerical quantification is and remains one of the most miraculous apparatuses that nature has ever created."

Herbert Spencer (1872):

"Spatial relationships have been the same, not only for all men, all primates and all orders of mammals from which we descend, but also for all orders of less elevated beings". They are "expressed in defined nervous structures, congenitally constituted to act in a certain way, and incapable of acting in a different way".

Brain and Mathematics

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Helen De Cruz (2006):

"The philosophy of mathematics has not paid much attention to the biological context of mathematics, although it goes without saying that mathematicians are biological organisms and that they produce mathematical theories and practices with their brains."

Culture and Mathematics

By reducing the mind to the brain and the intellectual development to brain maturation, many authors have confused an individual brain functioning with the historical and collective evolution of scientific discourse, which is memorized in books (and stored in libraries) and obeys to Boolean logic.

Fernand Doridot & Marco Panza 2004b

"the men [and women] who ... managed to constitute abstract objects, and thereby constituted mathematical theories, are ... men [and women] in the plural, concrete men [and women] acting in historically determined conditions, and not sorts of excrescences of a "cognitive subject" ".

Fernand Doridot & Marco Panza 2004a

"The constitution of a mathematical theory is a historical fact ... it is the business of a few mathematicians working under determined conditions rather than the realization of a cognitive process specific to the species. And if, ..., it is so, then only history can account for this constitution and explain it ... The constitution of a mathematical theory seems to us difficult to conceive other than as a historical process, at least historically situated and determined."

Sylvain Auroux (1998)

Cognitive structures are external to the individual. They "depend on external instruments (books, libraries, calculation and observation instruments, etc.) as well as on social structures for the production and accumulation of knowledge (encyclopedias, learned societies, etc.) ... knowledge is a whole process at the same time material, social and collective, never limited, locked up, preserved or produced by individual skills which concern only moments and fragments of it"

Trends in Cognitive Sciences | **ColPress**

REVIEW
The Evolutionary History of Brains for Numbers
Andreas Nieder^{1,*}
Trends in Cognitive Sciences 2021

REVIEW
The Adaptive Value of Numerical Competence
Andreas Nieder^{1,*}
Trends in Ecology and Evolution 2020

Available online at www.sciencedirect.com
ScienceDirect | **Current Contents in Neurobiology**

Neural constraints on human number concepts
Andreas Nieder
Current Opinion Neurobiology 2020

Letter
Number Faculty Is Rooted in Our Biological Heritage
Andreas Nieder^{1,*}
Philosophical Trans. Royal Soc. 2017
Trends in Cognitive Sciences 2017

Evolution of cognitive and neural solutions enabling numerosity judgements: lessons from primates and corvids
Andreas Nieder
Philosophical Trans. Royal Soc. 2017

The neuronal code for number
Andreas Nieder
Nature Reviews Neuroscience 2016

REVIEW
Coding of abstract quantity by 'number neurons' of the primate brain
Andreas Nieder
Journal of Comparative Physiology 2013

Representation of Number in the Brain
Andreas Nieder¹ and Stanislas Dehaene²
Annual Review Neuroscience 2009

A parieto-frontal network for visual numerical information in the monkey
Andreas Nieder^{*} and Earl K. Miller
PNAS 2004

Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex

Oana Tudusciuc and Andreas Nieder^{*}
PNAS 2007

Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex

Oana Tudusciuc and Andreas Nieder^{*}
PNAS 2007

Between Q=2 and Q=3
 $\Delta(2,3) < 1$ spike/s
0,1 spike/100 ms
0,6 spike/600 ms

Between Q=3 and Q=4
 $\Delta(3,4) < 2$ spikes/s
0,2 spike/100 ms
1,2 spike/600 ms

Among the numerous spikes they receive from pre-synaptic neurons during 600 milliseconds, how do the post-synaptic neurons manage to distinguish the few spikes emitted by this neuron from the spikes emitted by other pre-synaptic neurons and enable the monkey to produce different responses according to the number of stimuli ?

Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex

Oana Tudusciuc and Andreas Nieder^{*}
PNAS 2007

Between Q=2 and Q=3
 $\Delta(2,3) = 1$ spike/s
0,1 spike/100 ms
0,5 spike/600 ms

Between Q=3 and Q=4
 $\Delta(3,4) = 2$ spikes/s
0,2 spike/100 ms
1,2 spike/600 ms

Out of the numerous spikes they receive from pre-synaptic neurons during 600 milliseconds, how do the post-synaptic neurons manage to distinguish the few spikes emitted by this neuron from the spikes emitted by other pre-synaptic neurons and enable the monkey to produce different responses according to the number of stimuli ?

Between Q=2 and Q=3
 $\Delta(2,3) = 2$ spikes/s
0,2 spike/100 ms
1,2 spike/600 ms

Between Q=3 and Q=4
 $\Delta(3,4) = 4$ spikes/s
0,4 spike/100 ms
2,4 spike/600 ms

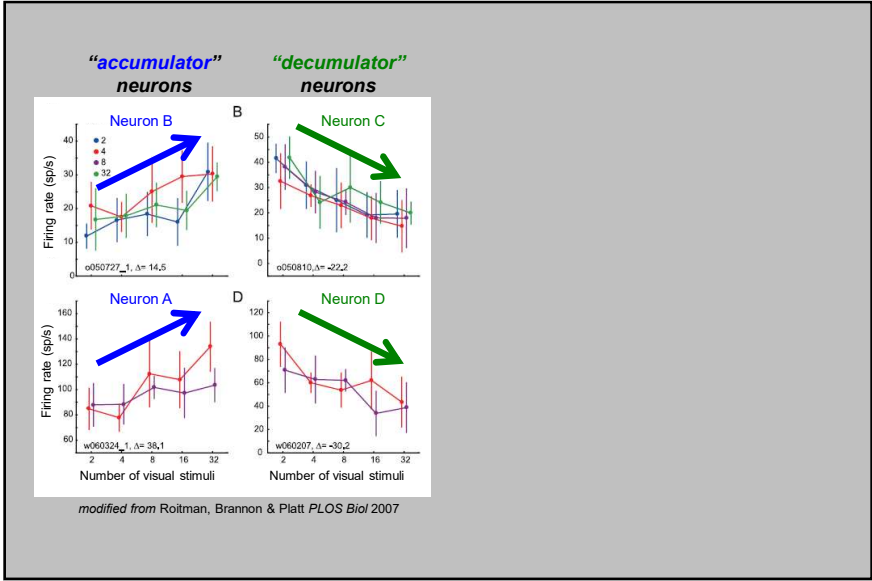
OPEN ACCESS Freely available online PLOS BIOLOGY

Monotonic Coding of Numerosity in Macaque Lateral Intraparietal Area

2007

Jamie D. Roitman^{1*}, Elizabeth M. Brannon^{2,3}, Michael L. Platt^{1,3}

1 Department of Neurobiology, Duke University, Durham, North Carolina, United States of America, 2 Department of Psychology and Neuroscience, Duke University, Durham, North Carolina, United States of America, 3 Center for Cognitive Neuroscience, Duke University, Durham, North Carolina, United States of America



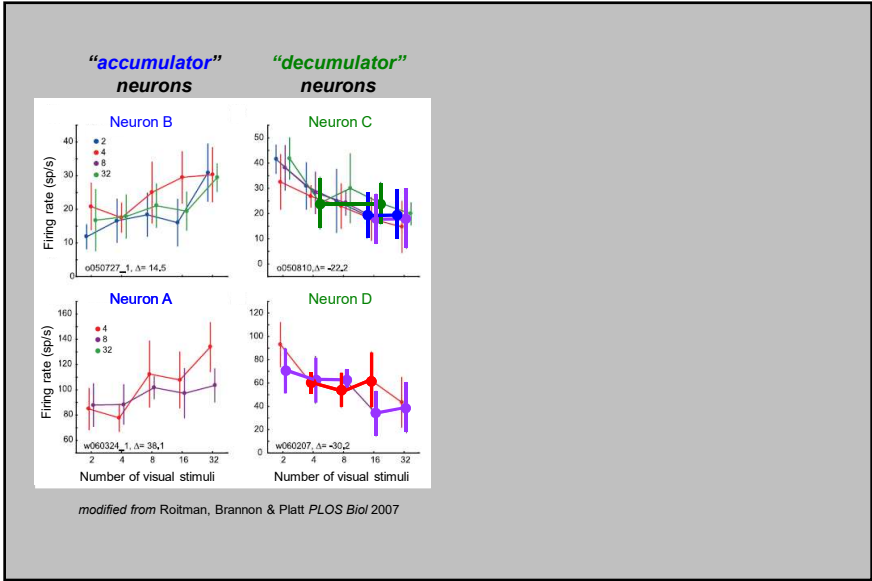
How do post-synaptic neurons "distinguish" whether 4, 8 or 16 stimuli were presented in the response field of the recorded neuron ?

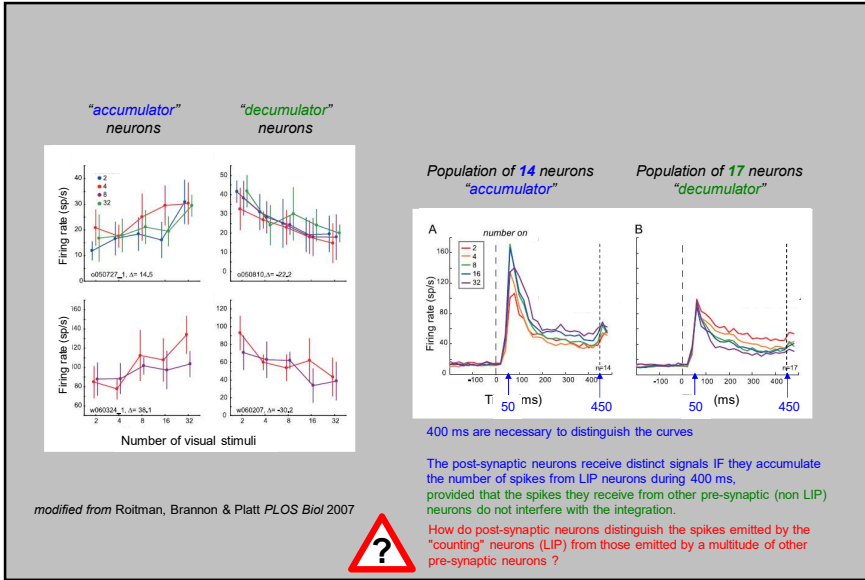
Neuron B :
During task 32, the post-synaptic neurons cannot "distinguish" whether 2-4-8 or 16 stimuli were presented in the response field of the recorded neuron.
During task 2, they receive no signal enabling them to "distinguish" whether 4, 8 or 16 stimuli were presented.

Neuron A :
During task 8, the post-synaptic neurons (targeted by neuron A) cannot distinguish whether 8-16 or 32 stimuli were presented in the response field of the recorded neuron. They receive cannot distinguish either whether 2 or 4 stimuli were presented.
During task 4, the post-synaptic neurons cannot distinguish whether 8 versus 16 (or 2 versus 4) stimuli were presented.

How do the post-synaptic neurons distinguish whether 8, 16 or 32 stimuli were presented in the response field of the recorded neuron ?
 How do they distinguish whether 2 or 4 stimuli were presented ?

modified from Roitman, Brannon & Platt PLOS Biol 2007



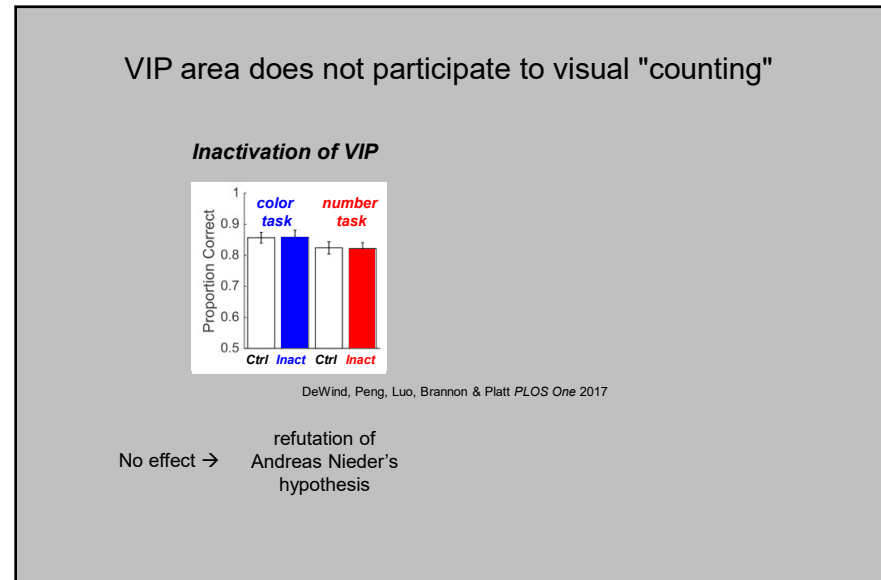
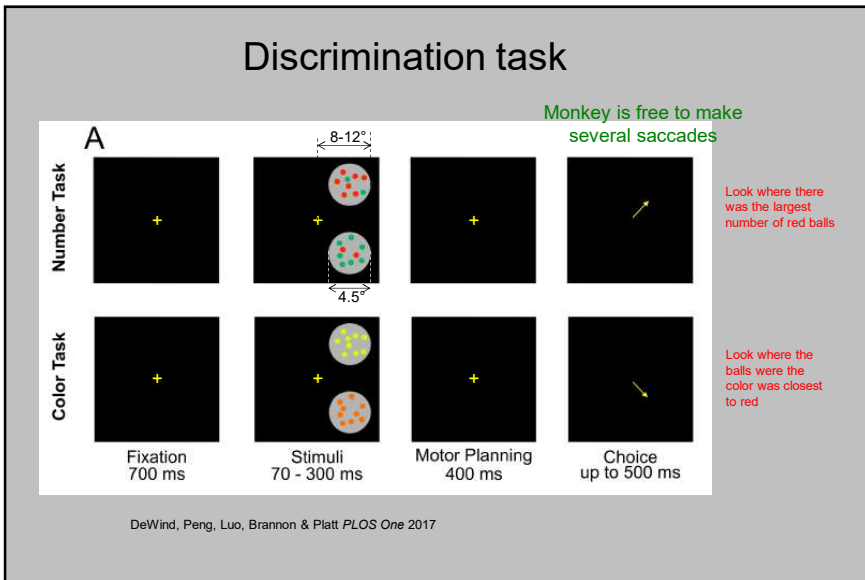


A correlation between the firing rate of neurons and an external event (i.e., number of items in the visual field) does not necessarily imply that the spikes contribute to the behavioral response.

Pharmacological inactivation does not support a unique causal role for intraparietal sulcus in the discrimination of visual number

Nicholas K. DeWind^{1,2}, Jiyun Peng², Andrew Luo³, Elizabeth M. Brannon¹, Michael L. Platt^{1,4,5}

PLOS One 2017

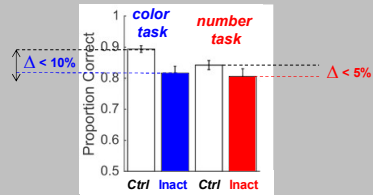


LIP area does not participate to visual "counting" either

Inactivation of VIP



Inactivation of LIP



DeWind, Peng, Luo, Brannon & Platt PLOS One 2017

No effect → refutation of Andreas Nieder's hypothesis

Fallacious logic

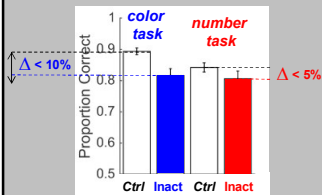
According to DeWind, Peng, Luo, Brannon & Platt (2017), if LIP and VIP areas are specialized in processing the number of visual items, THEN inactivation of either of these areas should cause a greater deficit in a numerical discrimination task than in a color discrimination task.
→ We have seen that this is not the case

Instead of rejecting the premises, i.e., instead of concluding that LIP and VIP areas play no role in processing the number of visual items, they propose another inference :

IF inactivation leads to similar deficits in both tasks (numerical and color discrimination) THEN the numerical processing in LIP and VIP areas is the mere signature of a general purpose circuit for ordinal comparison, visual attention or perceptual decision making

Simpler explanation

Inactivation of LIP



The small drops of performance 8% (color discrimination) and 4% (quantitative discrimination) may result from a mild visual impairment (diplopia, ocular divergence, etc.?).

DeWind, Peng, Luo, Brannon & Platt PLOS One 2017

Journal of Neurophysiology

Neurons in Monkey Parietal Area LIP Are Tuned for Eye-Movement Parameters in Three-Dimensional Space

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Journal of Neurophysiology 1995

Conclusion

There is no evidence in the monkey indicating an involvement of the parietal cerebral cortex in numerical "cognition".

In humans, brain imaging studies unfortunately say nothing about the firing rate of neurons, their timing and their transmission. The fMRI-BOLD signal reflects pre-synaptic activity and not the emission of action potentials (Lippert et al. *Magnetic Resonance Imaging* 2010).

During the last decades, confusions were made in domain of cognitive neuroscience between

- the measurements (measured values and their numerical transformations),
- the physiological processes that generate the measured phenomenon and
- the concepts

The limitations of measurements and the associated theoretical notions led the community of cognitive neuroscientists (authors, **reviewers, popularizers and teachers**) to promote a nativist and evolutionary option, such as a coding in the brain of space, time, numbers, Geometry and Arithmetic.

They neglected the fact that a multitude of cognitive structures are external to the individual, i.e., the "external instruments (books, libraries, calculation and observation instruments...) and the social structures of production and knowledge accumulation (encyclopedias, learned societies, etc.)" (Sylvain Auroux 1998).

"Mathematics is a collective work of art that derives its objectivity through social interactions" (Yehuda Rav 1988)

"The locus of scientific rationality is not the individual scientist but the scientific community" (Miriam Solomon 1996)

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THESE DE DOCTORAT

Soutenu(e) à Aix-Marseille Université

le 14 décembre 2022 par

Laurent Goffart

Le cerveau en trompe-l'œil des sciences cognitives : Critique du plongement dans le fonctionnement cérébral de notions qui lui sont étrangères

Discipline
Philosophie

École doctorale
ED 1563 Cognition, Langage, Éducation

Laboratoire/Unité de recherche
CEREAU - Centre de Recherche en Éducation et en Sciences Cognitives, Aix-Marseille Université
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- Université de Lille
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Cerebralization of the notion of space

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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 dogma, 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.

Behavioral and Brain Sciences 1986

Anciens dogmes et nouveaux axiomes en théorie du cerveau

Andras J. Pellionisz

Il n'y a peut-être pas de tâche plus importante pour une théorie dans n'importe quelle branche d'une science que de supprimer les anciens dogmes - ceux qui se sont avérés inappropriés mais qui persistent - et de les remplacer par de nouveaux axiomes. Cette tâche est extrêmement importante dans les neurosciences, qui subissent actuellement une métamorphose d'une science largement descriptive ("soft"), où les postulats de base sont considérés comme acquis, en une discipline exacte avec sa propre théorie mathématisée du cerveau, dans laquelle les axiomes doivent être explicites. L'identification des postulats fondamentaux implicites, suivi de l'adoption des axiomes appropriés et de la suppression des dogmes inappropriés, est un travail des plus difficiles et souvent ingrat. Le terrain doit néanmoins être déblayé si l'on veut construire une théorie mathématique solide du cerveau sur la base d'un ensemble d'axiomes nouvellement établis.