Sensori-motor learning in the barrel cortex.

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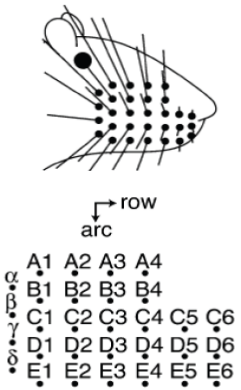
Outline

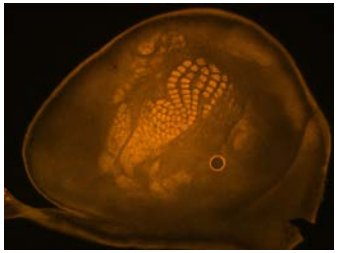
- Introduction
  - The rodent whisker system
  - Sensory maps
- I) Unsupervised learning leads to the late emergence of the direction selectivity map in the barrel cortex
- II) Superposition of functional maps in the barrel cortex
- III) Reinforcement learning of an active tactile task
- Conclusion

Introduction

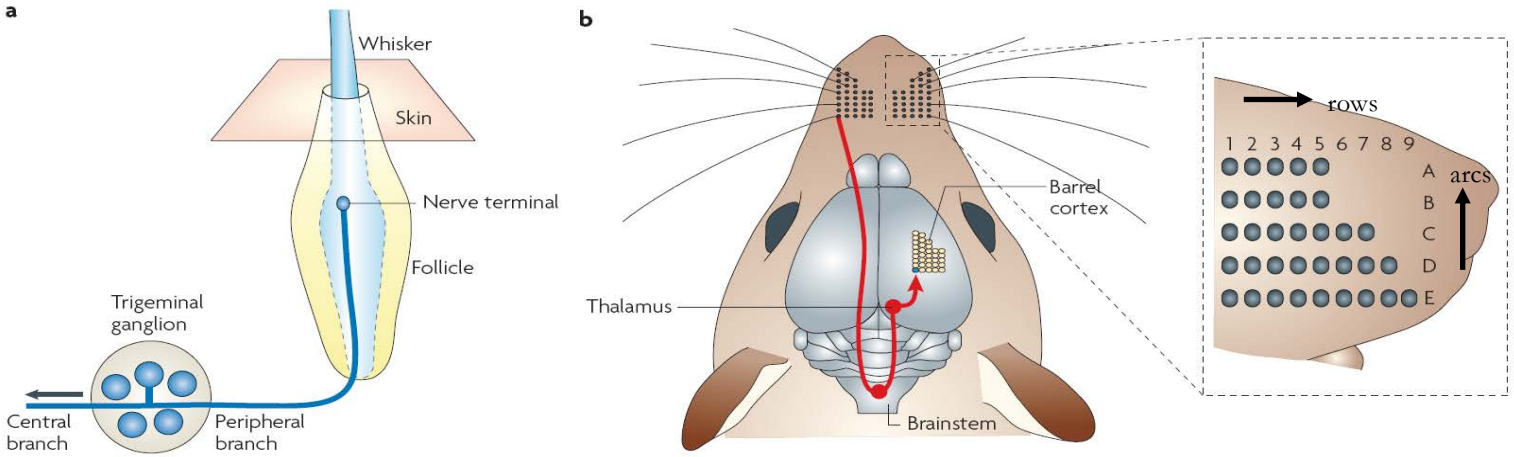


- **Localization of objects (in the dark) : WHERE**

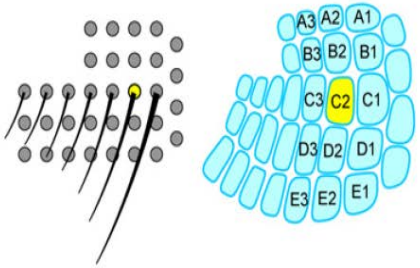
- **Information about object shape, size and surface texture: WHAT**



From whiskers to the somatosensory cortex



M. Diamond, Nature Rev. Neurosc. 2008

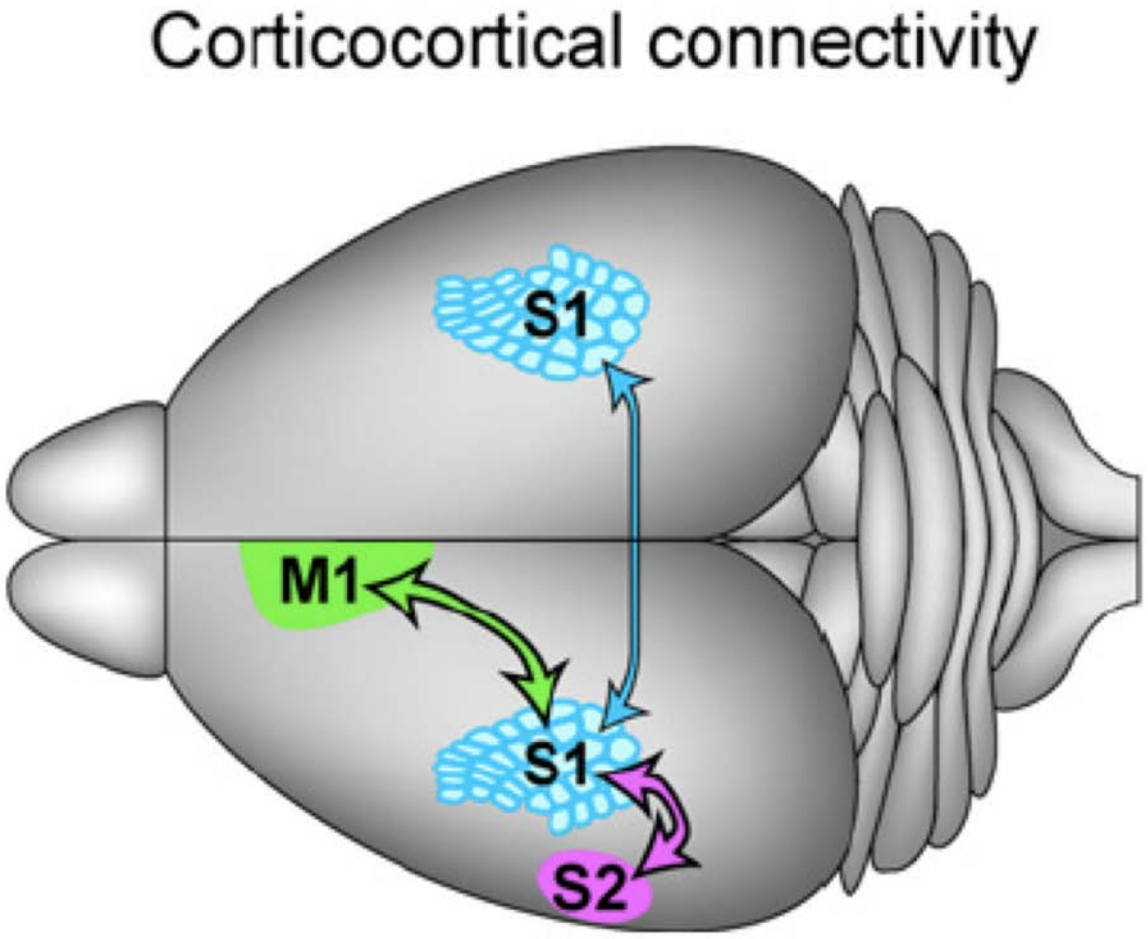


C. Petersen, Neuron 2007

Dominant paradigm for whisker processing of tactile information :

- Whiskers have discrete cortical representations
- Barrels are anatomically and functionally independent

From whiskers to the somatosensory cortex



C. Petersen, Neuron 2007

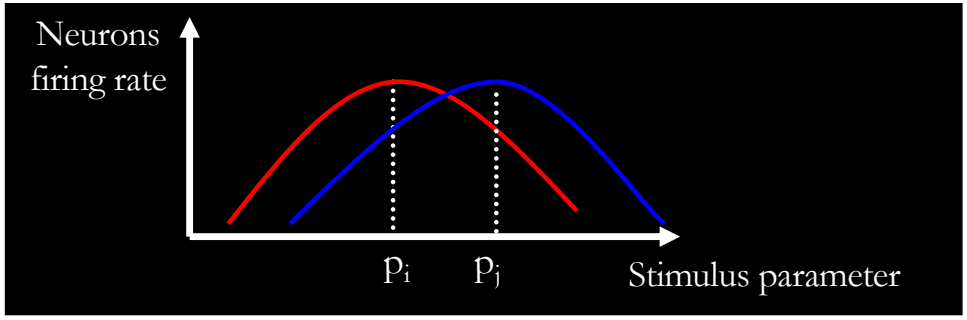
Cortical Columns in Rodent S1

	Rat		Mouse	
Column Size	**430 x 430 x 2000 µm** (C/D barrel)		**220 x 220 x 1150 µm** (C/D barrel)	
Layer	**Excitatory Ns**	**INs**	**Excitatory Ns**	**INs**
L1	10 ± 7	53 ± 6		26 ± 8
L2	1701 ± 484	338 ± 40	546 ± 49	107 ± 7
L3	3398 ± 807	338 ± 109	1145 ± 132	123 ±19
L4	4089 ± 425	358 ± 15	1656 ± 83	140 ± 9
L5	3267 ± 300	705 ± 93	1095 ± 96	221 ± 20
L6	4425 ± 320	427 ± 48	1288 ± 84	127 ± 9
Total	**16889** (± 423)	**2220** (± 198)	**5730** (± 444)	**744** (± 72)

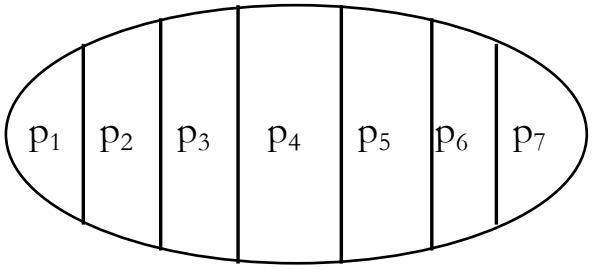
Hanno Meyer et al., PNAS *108*:16807-16812, 2008
Sandrine Lefort et al., NEURON *61*:301-316, 2009

Functional maps in the barrel cortex

Tuning curve : Neuronal response as a function of the value of a stimulus parameter

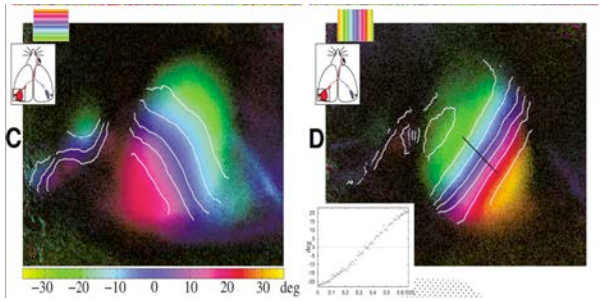


Maps : Domains in which neurons are tuned to the same value of the stimulus parameter



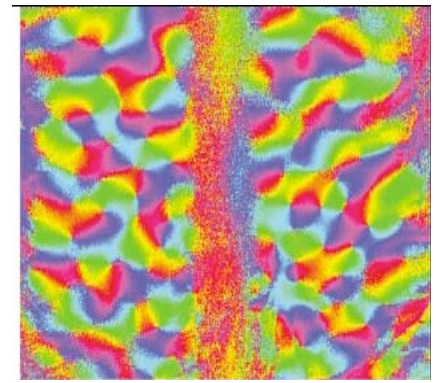
Functional maps are encountered in many cortical areas

Visual cortex



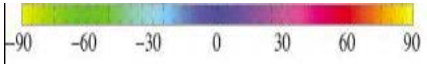
Position maps
(elevation and azimuth)
in the rat visual cortex.

Kalatzky Neuron 38 (2003) 529



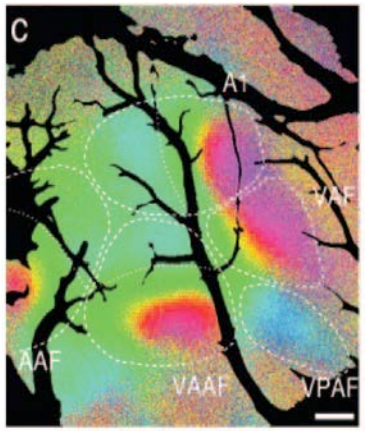
Orientation map
in the cat visual cortex.

Kalatzky Neuron 38 (2003) 529



Direction selectivity

Auditory cortex



Kalatsky PNAS 102 (2005) 13327

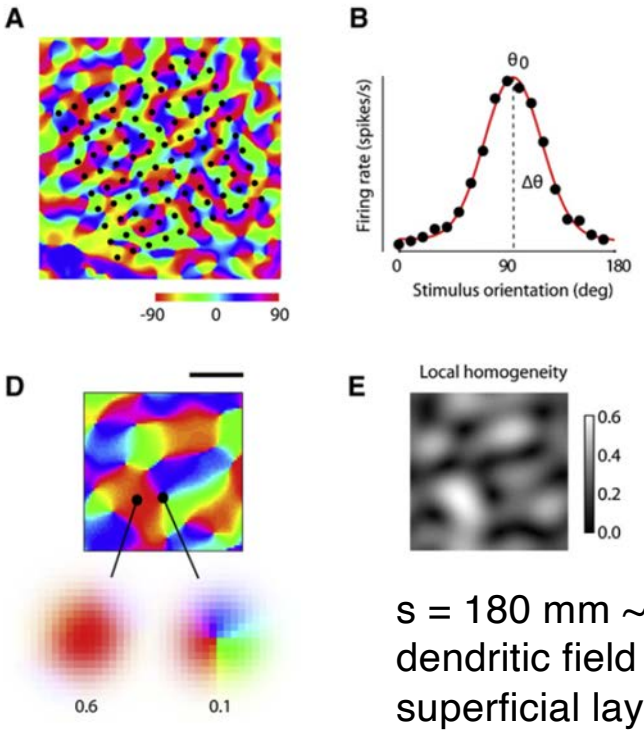
Frequency bands in the
rat auditory cortex.

Maps are **mesoscopic landmarks** at the surface of the cortex,

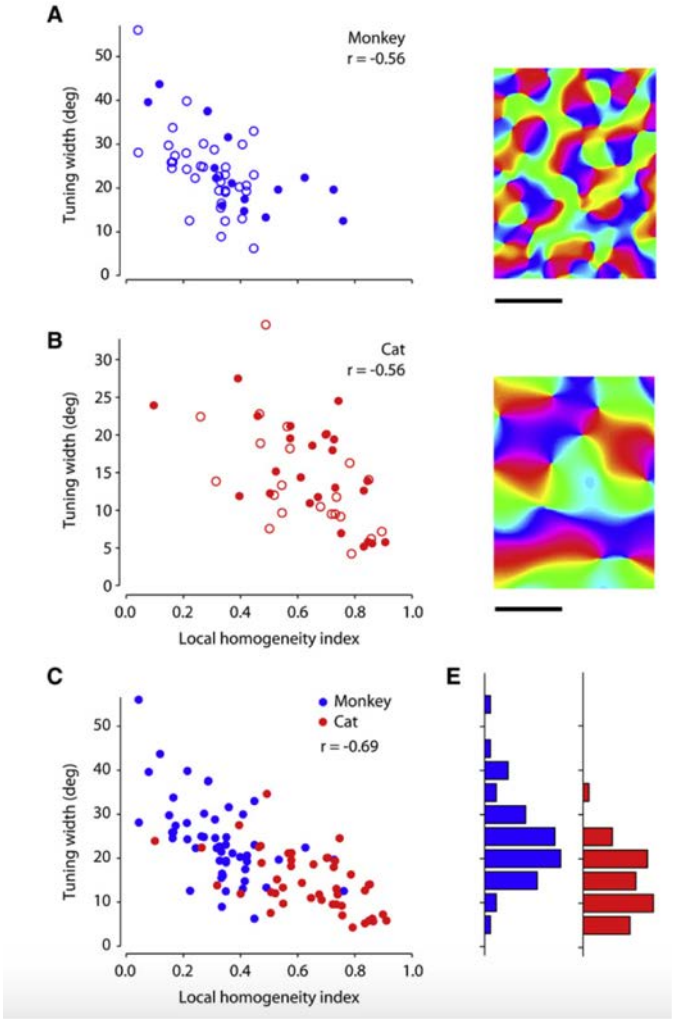
- **Easy to visualize** by different methods
- Allow thus to analyze the consequences of **developmental disorders**, **sensory deprivation**, **learning** etc…

Possible role of functional maps

Link between domain size and tuning strength



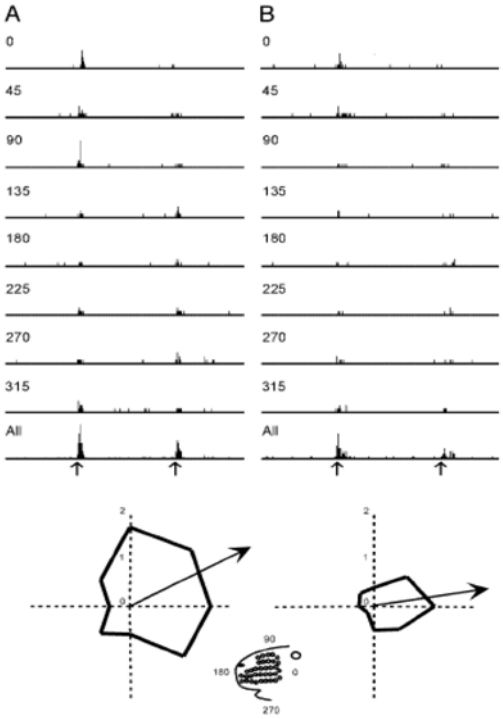
s = 180 mm ~ the dendritic field size of superficial layer neurons



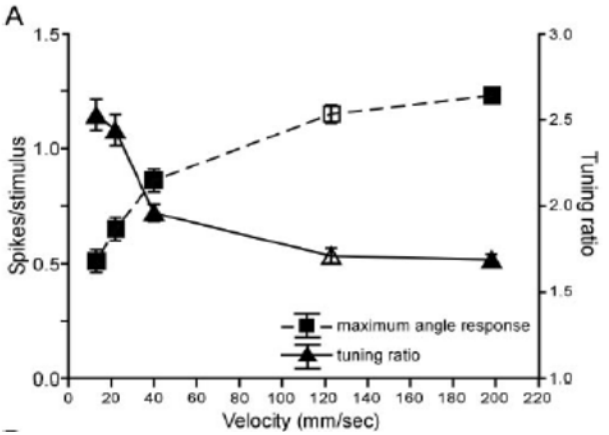
Nauhaus Neuron 2008

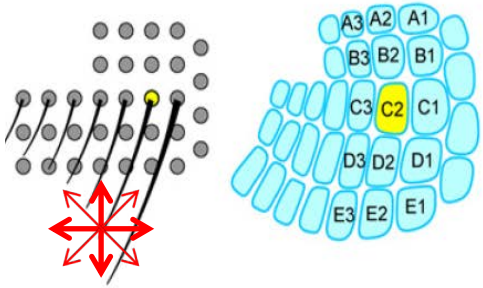
I) Late emergence of the direction selectivity map

Direction - selective cells
in the barrel cortex



Simons, 2004

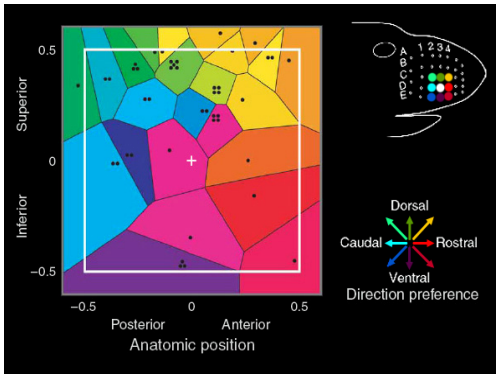




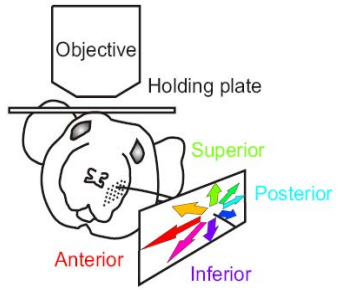
200mm/s (left)
40mm/s (right)

Ramp and Hold Stimulation

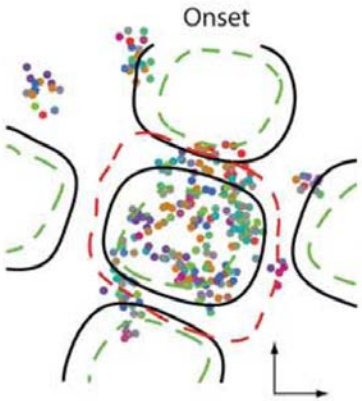
A controversial map



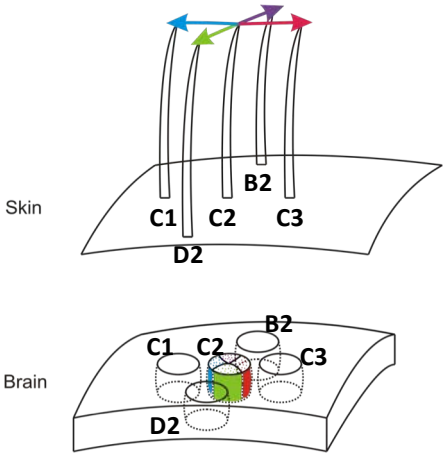
Andermann 2006



Radial organization of direction preference (pinwheel:)

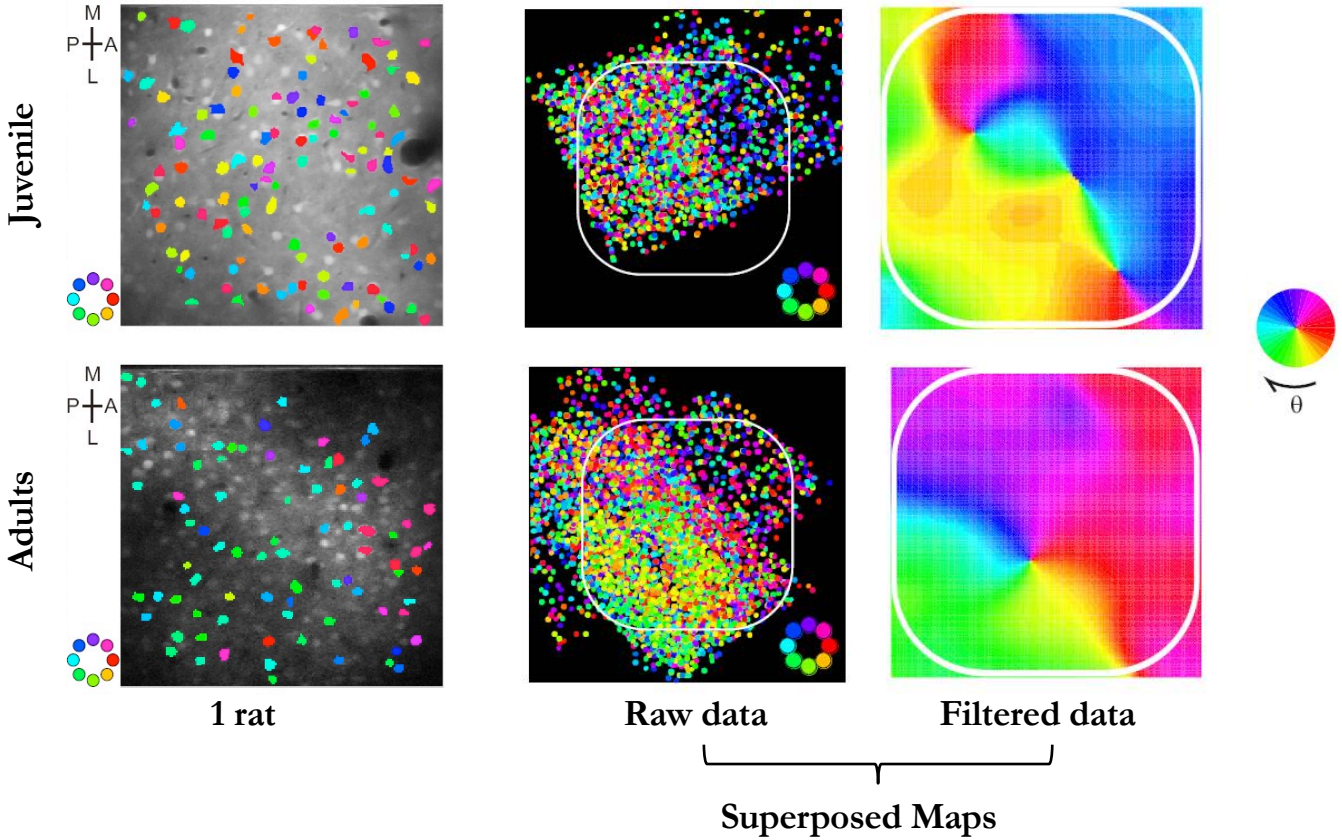


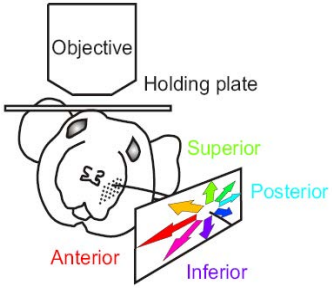
Kerr 2007



Absence of radial organization of direction preference

The direction map emerges in adult animals





Rats (juvenile and adults)
Oregon Green Ca Dye
Anesthetized
Acute

Kremer et al. *J. Neurosci.* 31(29) (2011) 10689-10700

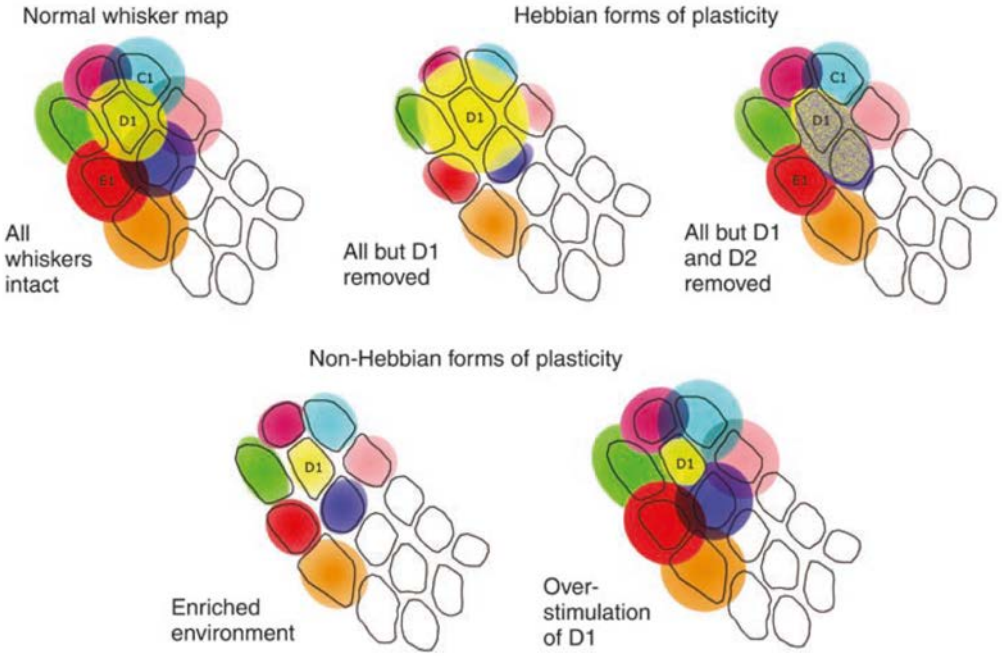
Early development of functional maps

- **Early development** of sensory cortical maps : **before the first postnatal month** in rodents.
  - Rodent, barrel field, layer 4 : a few days after birth (Inan and Crair, 2007; Petersen, 2007),
  - Rodent, barrel field, layer 2/3 receptive fields for vibrissa stimulation : 2 weeks postnatal (Stern et al., 2001).
  - Mouse, visual cortex, maps for visual space and ocular dominance : at eye opening (Smith and Trachtenberg, 2007).
  - Rat, auditory cortex AI, tonotopic map of sound frequency : 3 weeks postnatal (Zhang et al., 2002).
  - Cat, visual cortex, orientation map : before the end of the second postnatal week (Crair et al., 1998),
  - Ferret, visual cortex, direction selectivity map : just after the time of eye opening (Li et al., 2008).

- **Sensory activity** is known to **shape and strengthen sensory cortical maps** during **early postnatal life**:
  - Ocular dominance in the rodent visual cortex (Berardi et al., 2000; Smith and Trachtenberg, 2007)
  - Orientation and direction selectivity in the cat and ferret visual cortex (Crair et al., 1998; Li et al., 2008).

- Barrel cortex **direction selectivity map** emerges surprisingly **late**.
  - Could **plasticity** on its own be the **basis of the formation of the direction selectivity tactile map** ?
  - **Plasticity** is maintained **throughout life in the cortex** (Shulz and Frégnac, 1992; Karmarkar and Dan, 2006; Petersen, 2007).
  - **Activity-dependent plasticity in SIbf** both at the cellular level (Glazewski and Fox, 1996; Jacob et al., 2008) and at the scale of the barrel (Feldman and Brecht, 2005; Frostig, 2006).

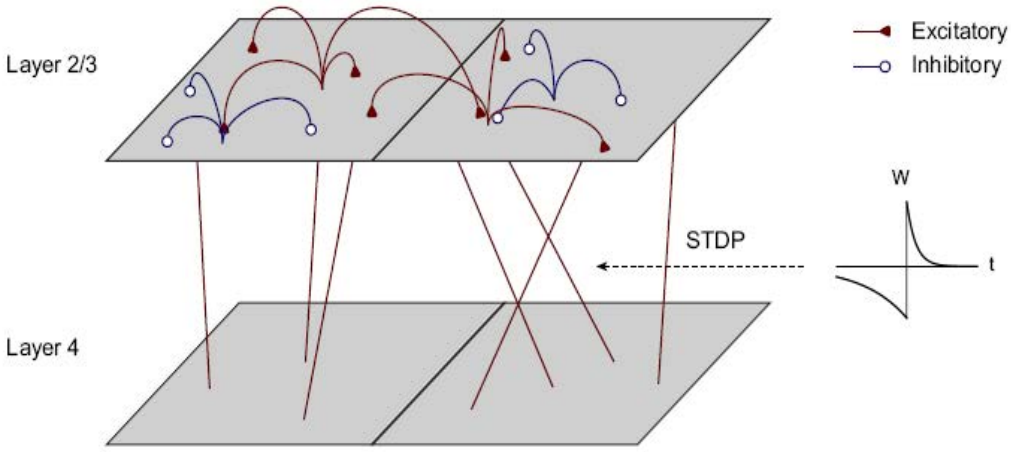
Functional maps



D. E. Feldman and M. Brecht,
Science 2005

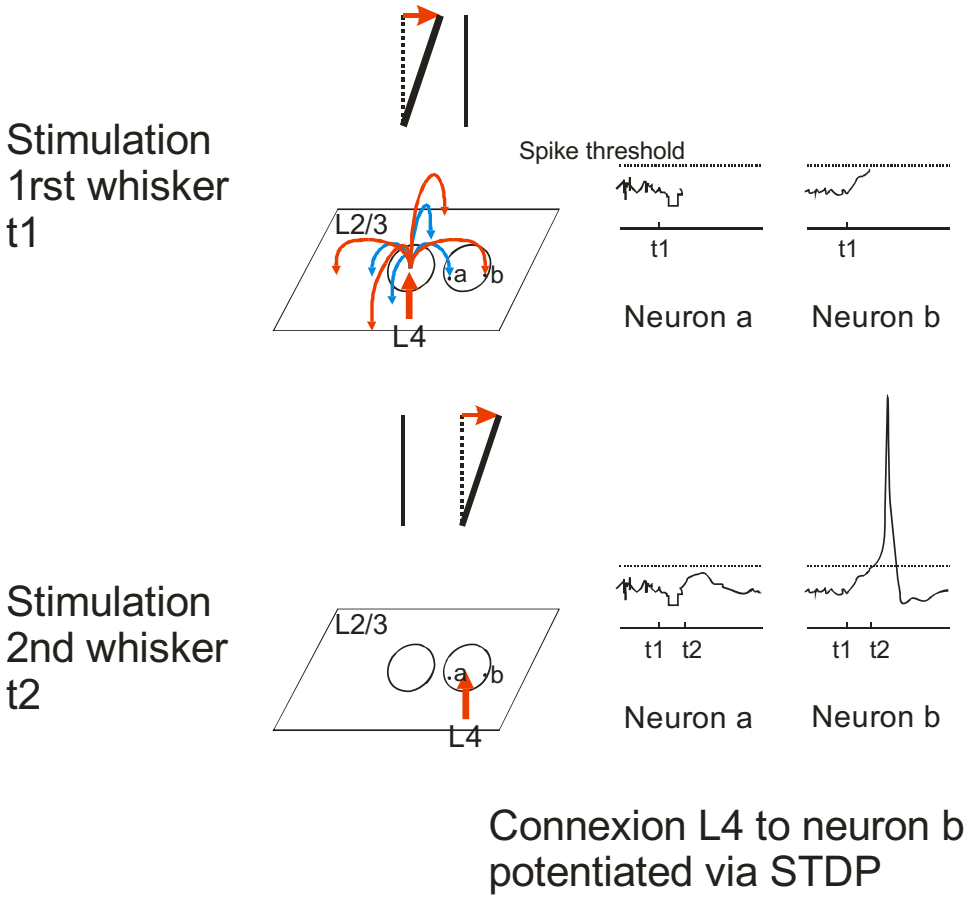
This map emerges trough sensory learning

- **Late (>P40) development** of the map
- **Map linked to the somatotopy**.
- **Link between direction of deflection and the somatotopy** ?
  An object deflects in a specific direction and successively neighboring whiskers
- **Numerical Model**
  Realistic network architecture + simple plasticity rules (STDP) at L4-L2/3 synapses + training



Dan Goodman, Romain Brette
DEC, ENS

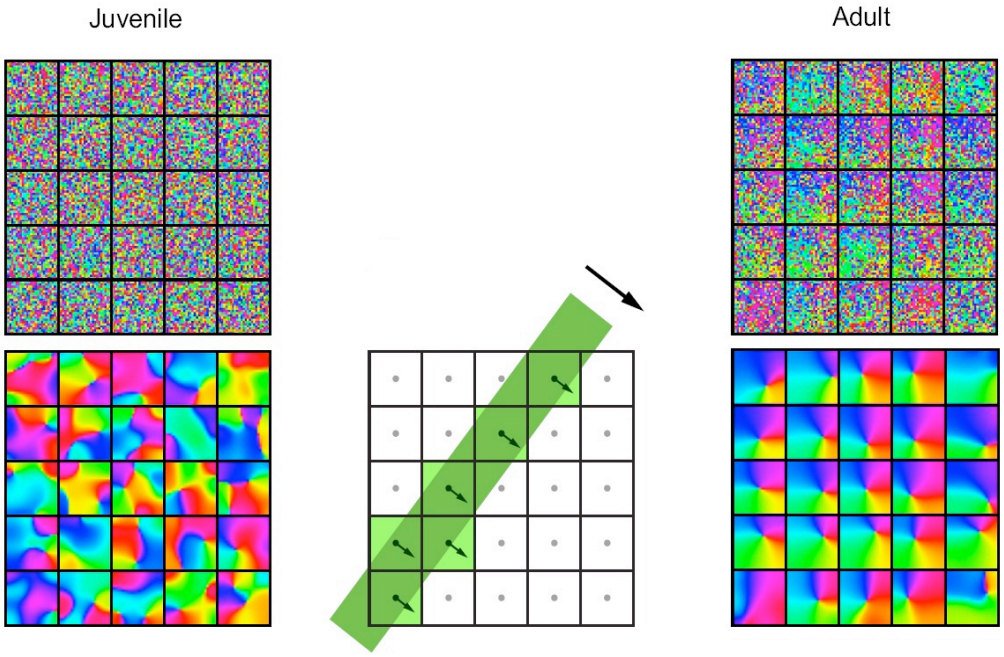
Network mechanisms underlying the map emergence

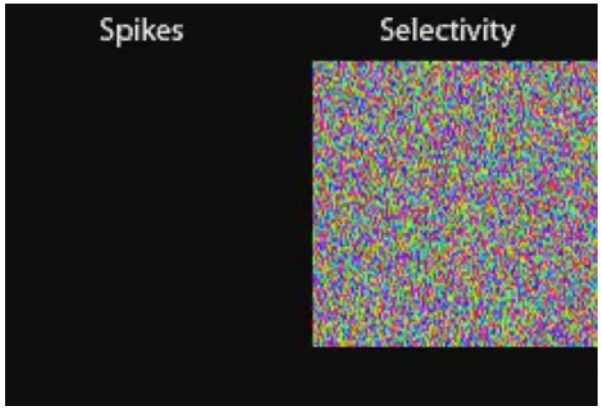


Connexion L4 to neuron b
potentiated via STDP

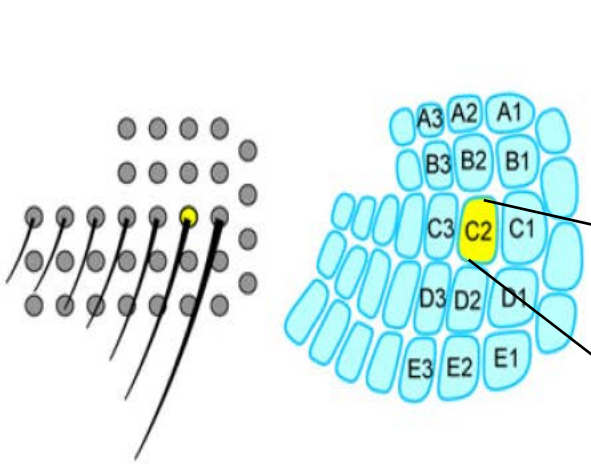
Sensory training induces the map formation

- Realistic neuronal network (L4-L2/3 and L2/3-L2/3 connections)
- Plasticity rule (STDP)
- Learning with natural stimuli (bars)



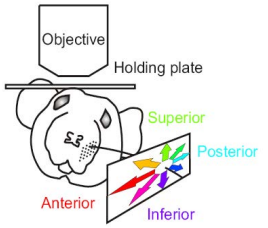


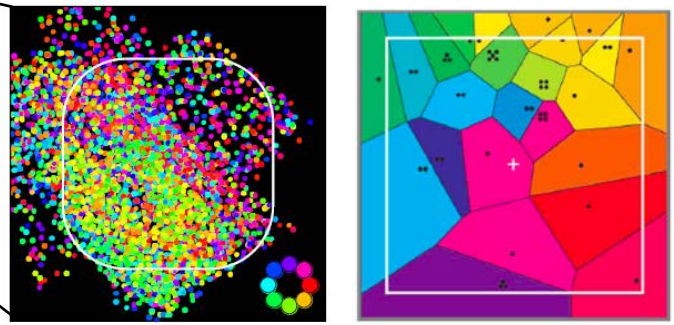
Functional maps in the barrel cortex



Barrels = map of whisker identity

Woolsey TA, Van der LoosH (1970) Brain Res 17:205–242.





Intra-barrel direction selectivity map

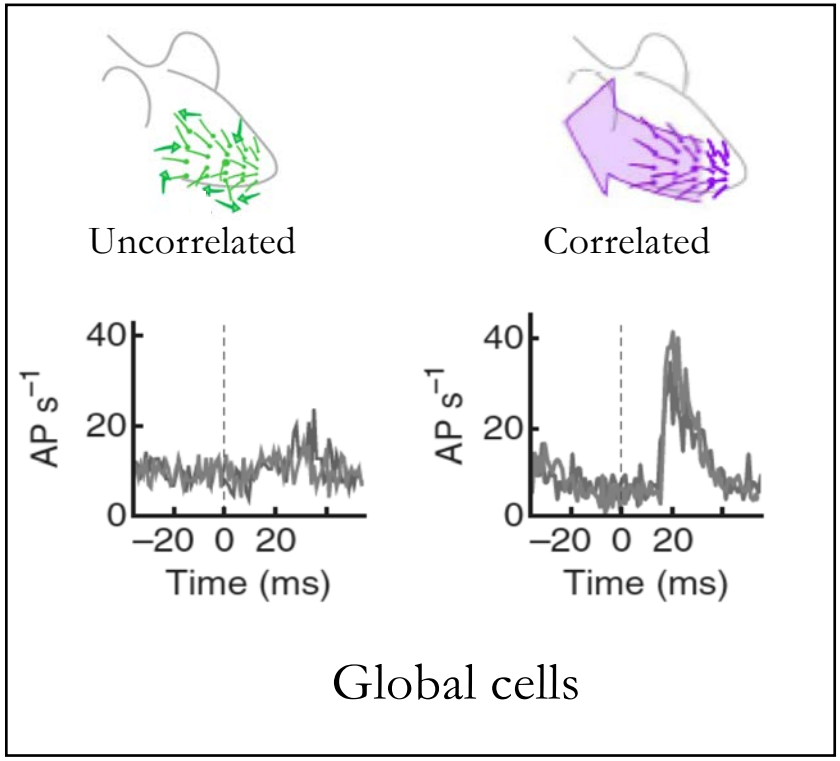
Late emergence in enriched environment

- Andermann ML, Moore CI (2006) Nat Neurosci 9:543.
- Kremer Y et al (2011) J Neurosci 31:10689.

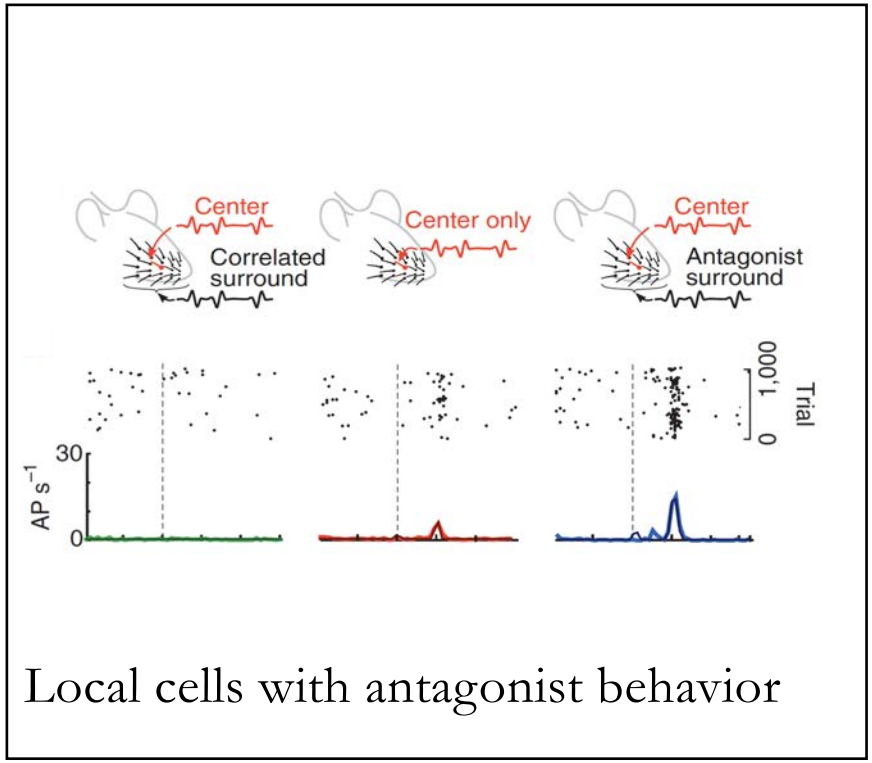
- a **surprisingly late development** after all known critical periods
- Direction selectivity maps reflect the **unsupervised learning of natural stimuli statistics**

II) Superposition of functional maps in the barrel cortex

Estebanez et al., Nat Neurosci, 2012



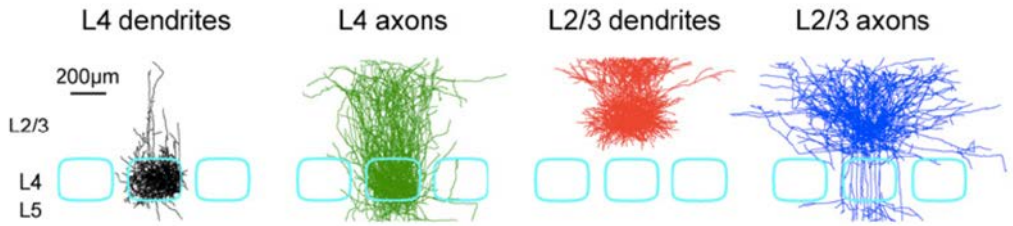
Global cells



Local cells with antagonist behavior

Highly non-linear responses to synchronous stimulations of several whiskers in Layers 4/5

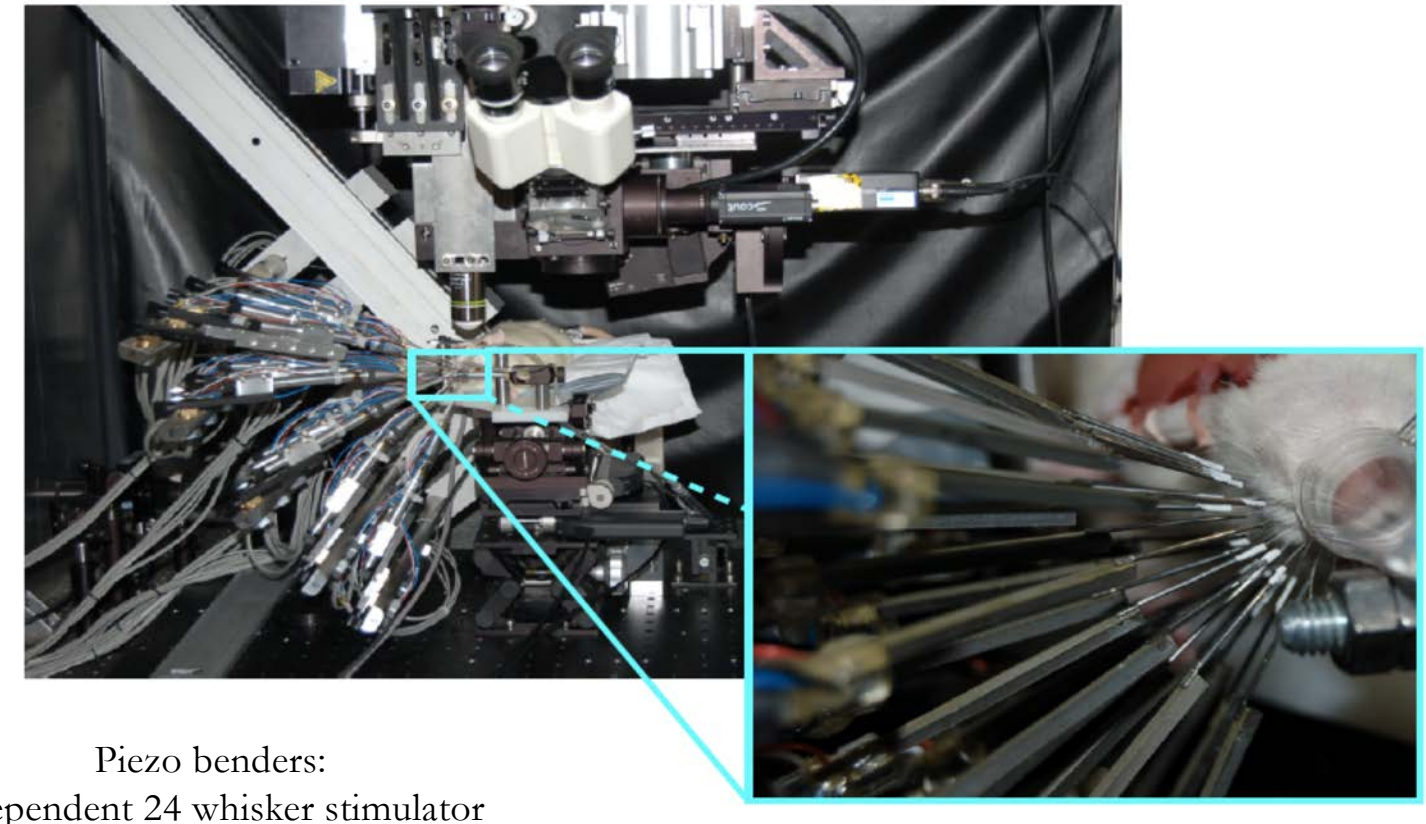
- Are they cells with a non-linear response to temporally correlated deflections of several whiskers in layer 2/3 ?



Petersen 2003

- Is there a specific functional mapping of such cells?
  - Naturalistic stimuli are multiwhisker : unsupervised learning
  - No map of the tuning to multi-whiskers correlations has been described.
  - How can multiwhisker correlated deflections be mapped on the barrel / septa map of single whiskers ?

A multi-whisker stimulation Matrix »

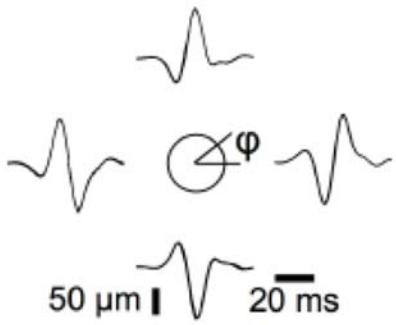


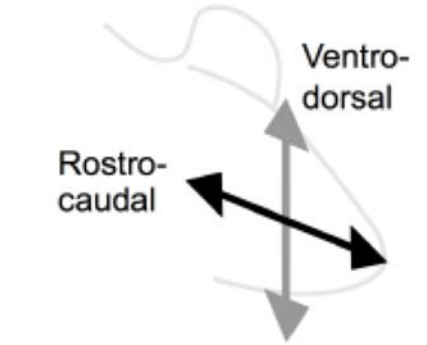
Piezo benders:
independent 24 whisker stimulator

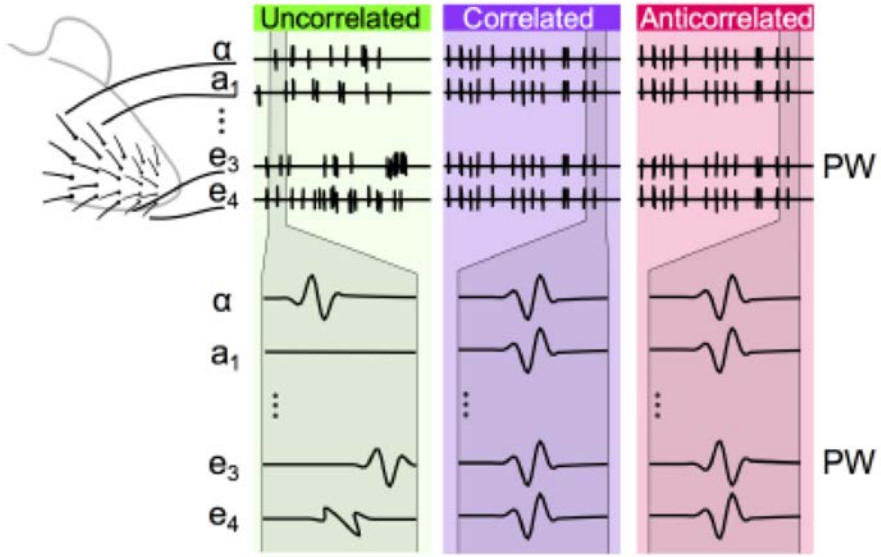
Daniel Shulz, UNIC, CNRS, Gif/Yvette

Complex, naturalistic stimulations

2 phases,
4 cardinal directions

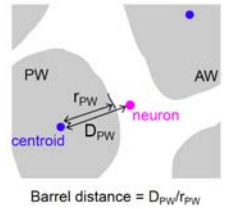


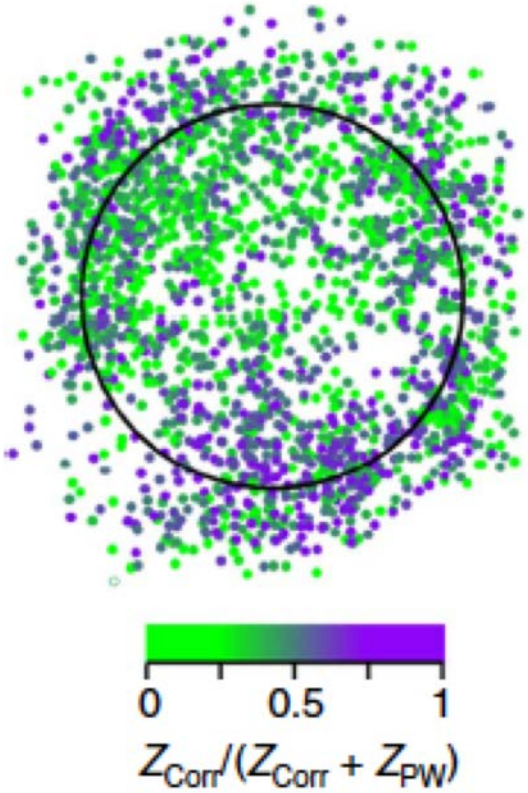


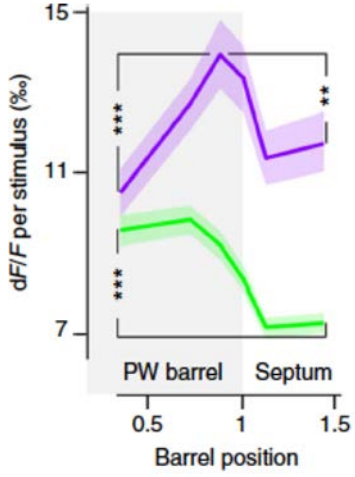


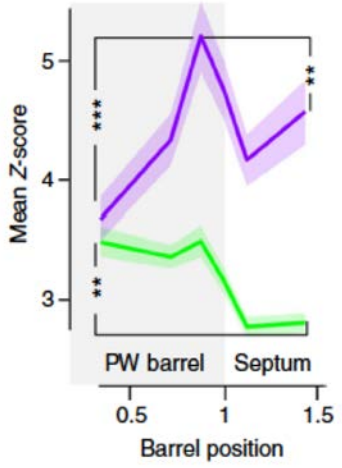
Only multiwhisker statistics varied with no change in single-whisker stimulus statistics.

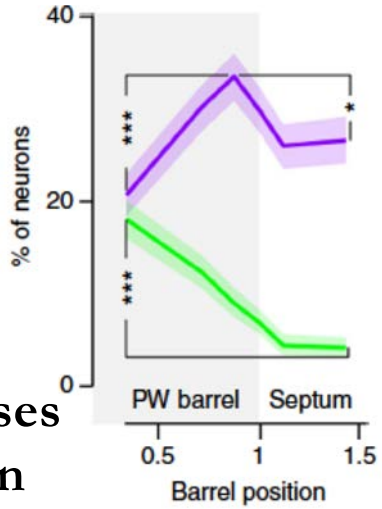
Mapping : a population analysis

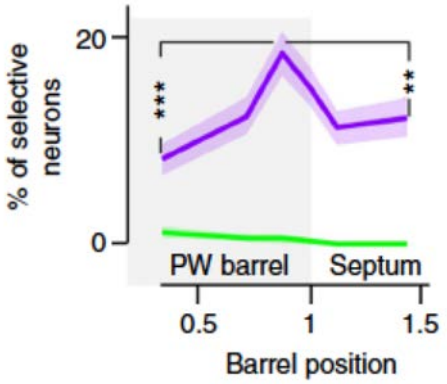






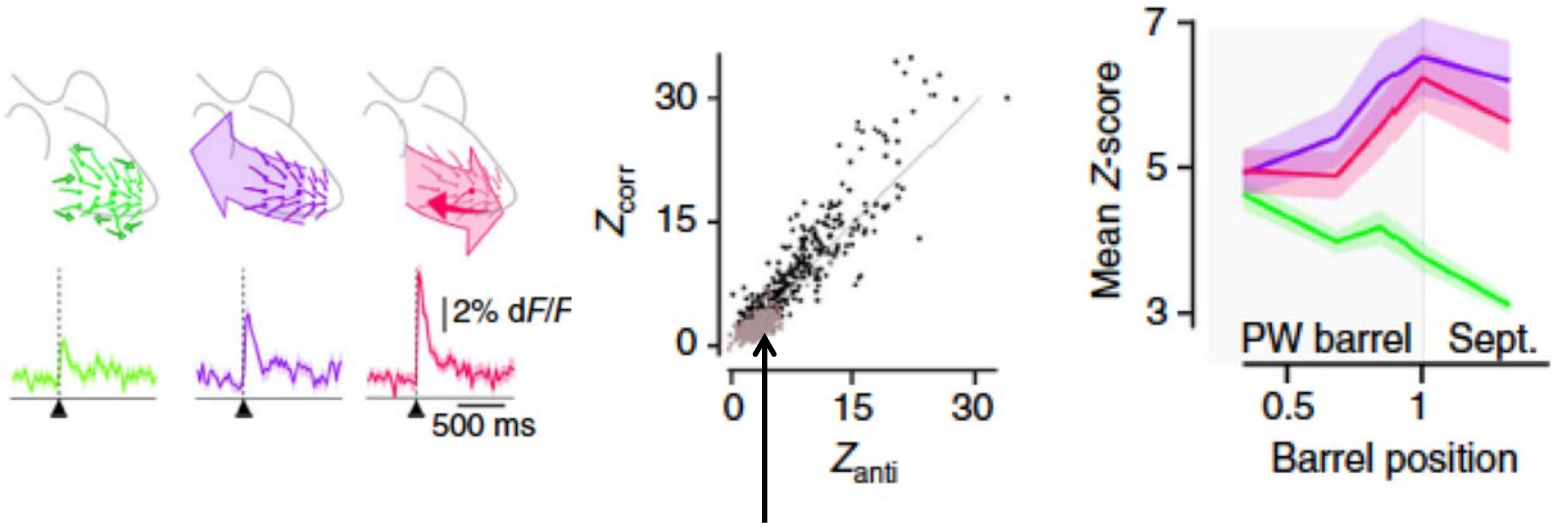






A concentric map of responses to multi-whisker correlation

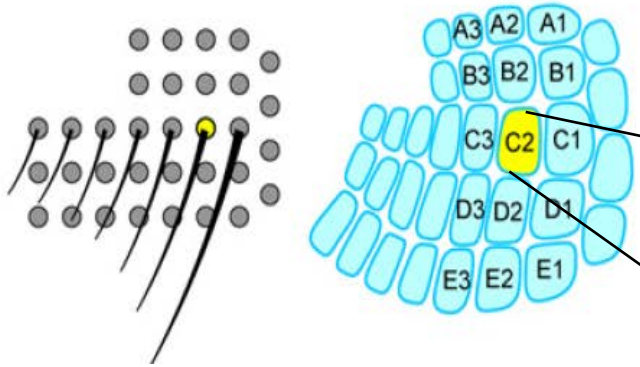
Selectivity to anticorrelated stimulations

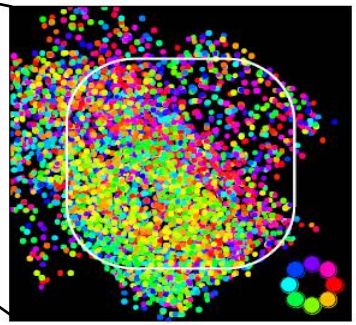


neurons preferring uncorrelated
over correlated stimulations

The ring is made of cells selective to the synchrony shared by the two multi-whisker stimulations (correlated and anti-correlated)

Functional maps in the barrel cortex

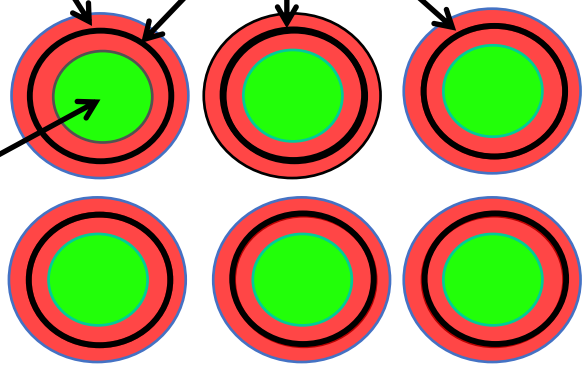




Cells selective to multi-whisker synchronous stimulations

Barrel borders

Cells selective to uncorrelated stimulations



At least 3 functional maps superimposed in the barrel cortex

III) Learning of a tactile information during an active tactile task

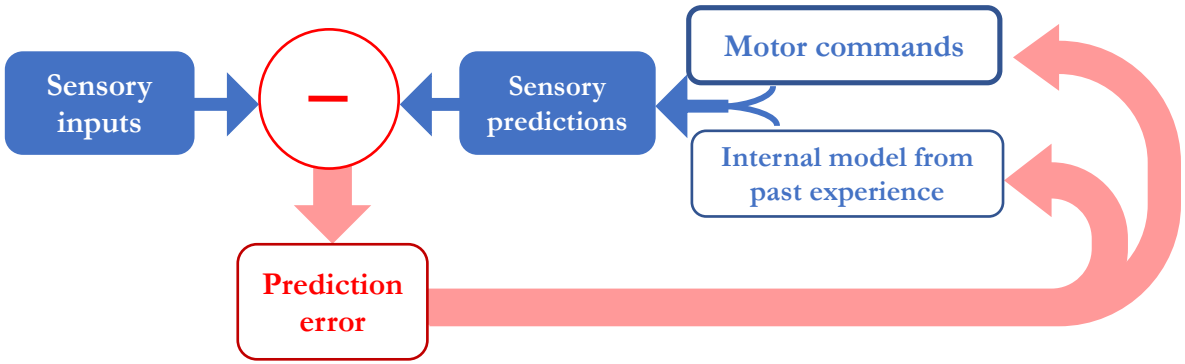
Tactile whisker perception are active tasks

Previous experiments were achieved anesthetized, but maps reflect active perception

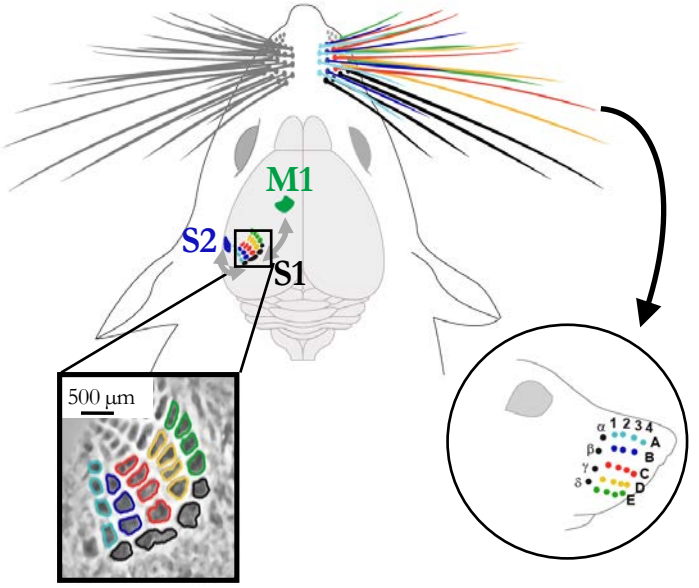
Reinforcement learning of tactile information

Neuronal mechanisms of the predictive coding during an active tactile sensorimotor task

Predictive Coding

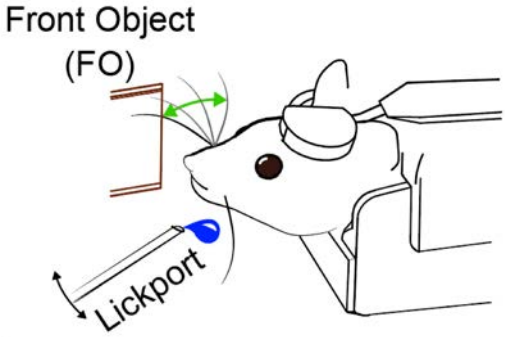


S1-S2-M1 circuit



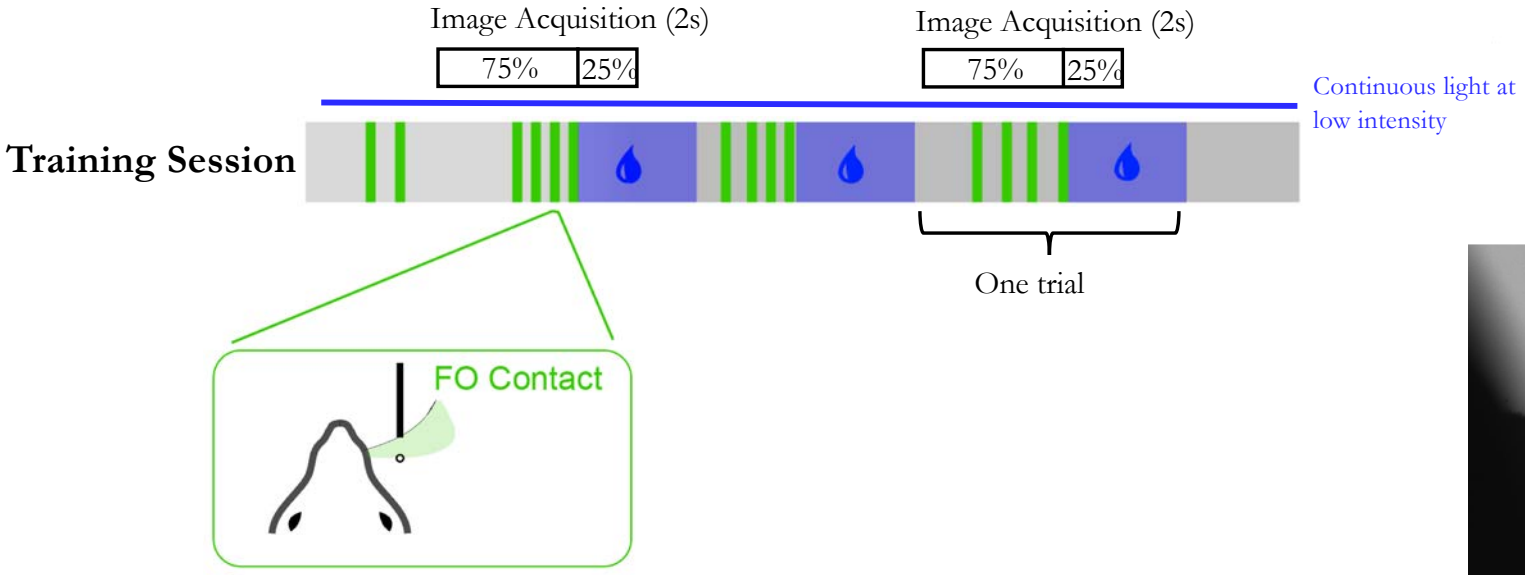
Primary somatosensory Cortex (layer IV)

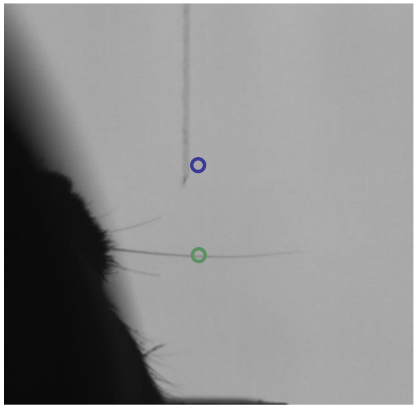
Task design



Object presence

Reward period





Progressive training from 2 to 4 consecutive FO **Big touches**
Inter contact time interval (300 ms)

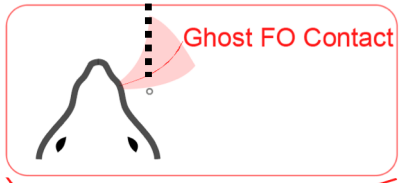
Recording of successive sessions with either Omissions or Mismatch touches

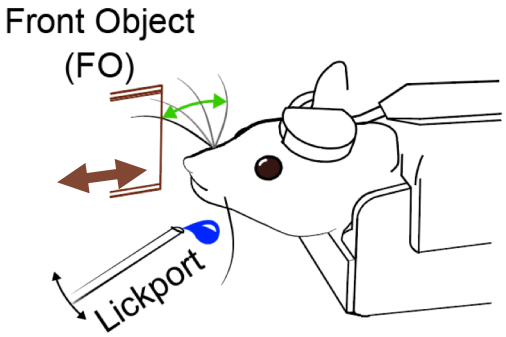
Object presence

Object absence

Reward period

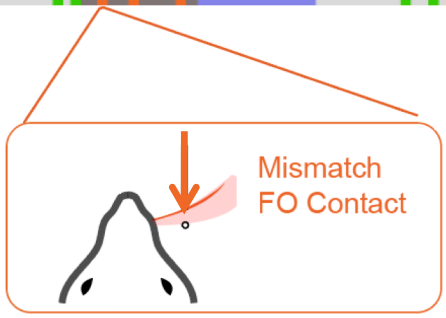
Object displacement





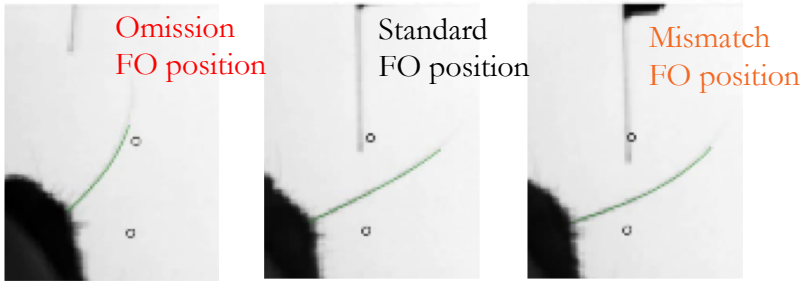
Omission Session
(10% violation trials)

Mismatch Session
(10% violation trials)

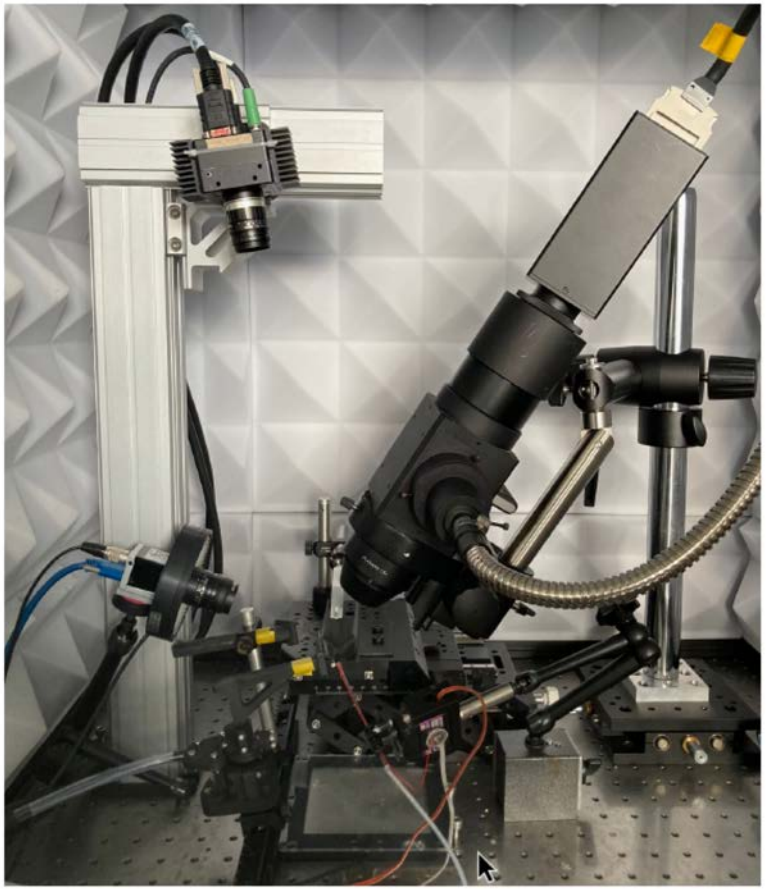


Mismatch distance

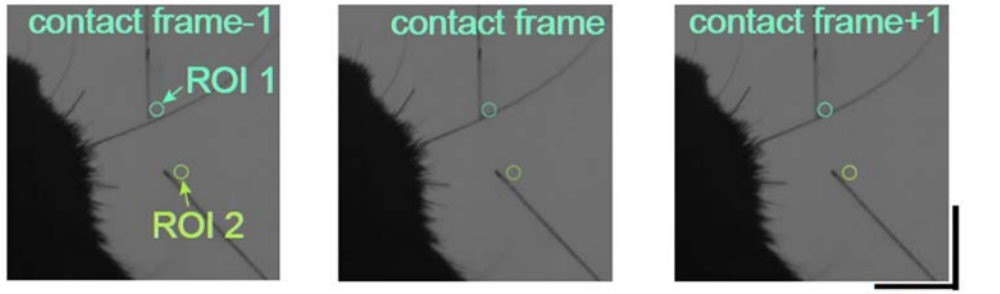
0.9 mm



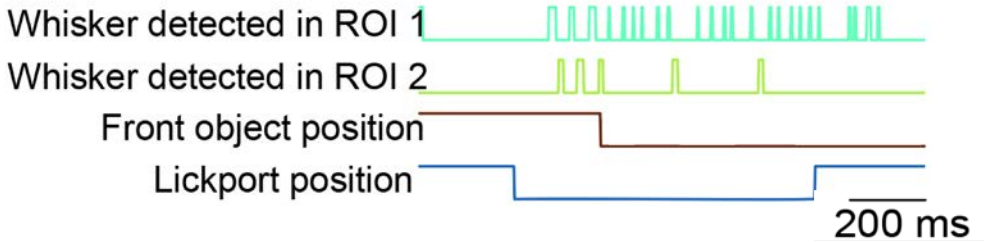
The behavioural task and the experimental setup



Robust real-time contact detection at 500 Hz

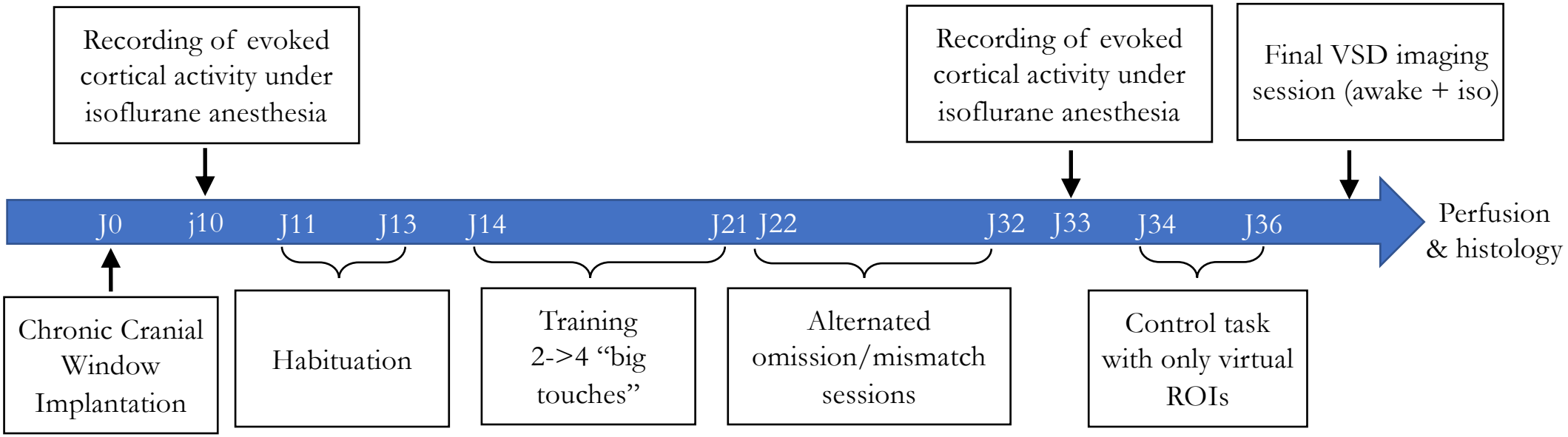


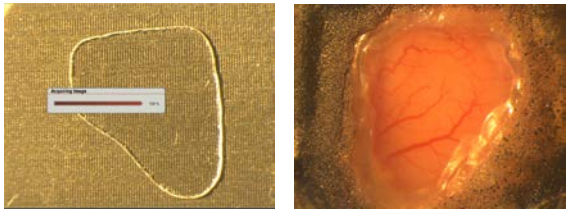
Setup signal acquisition
of one example VSD recorded omission trial



Displacement of the object is faster than half of the whisk cycle

Longitudinal chronic widefield Calcium imaging (GCaMP6f) through custom made large windows



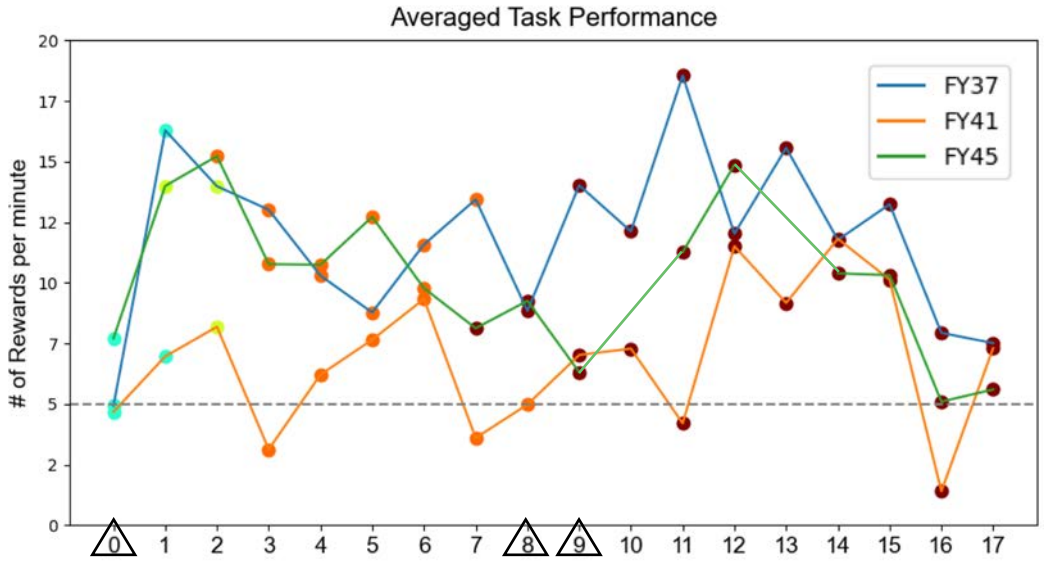


Laser cutting:
Institut Pierre-Gilles de Gennes

Learning curves

Number of required **consecutive** touches for one reward

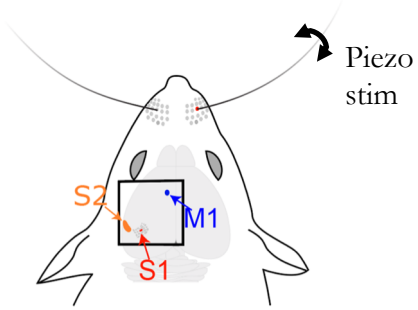
2 3 4 Omission/ Mismatch



Maximum 200 rewards or 40 minutes per session
Neural activity recording for each session
Multiple omission/mismatch session

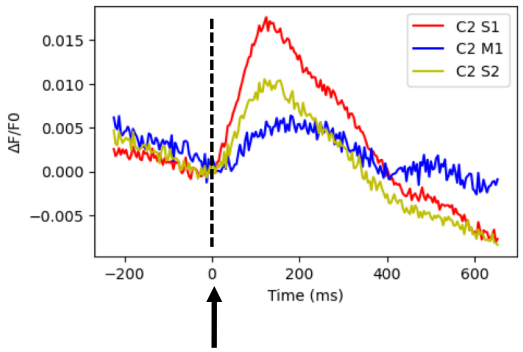
GCaMP functional imaging under anesthesia to localize cortical areas

C2 whisker stimuli under anesthesia



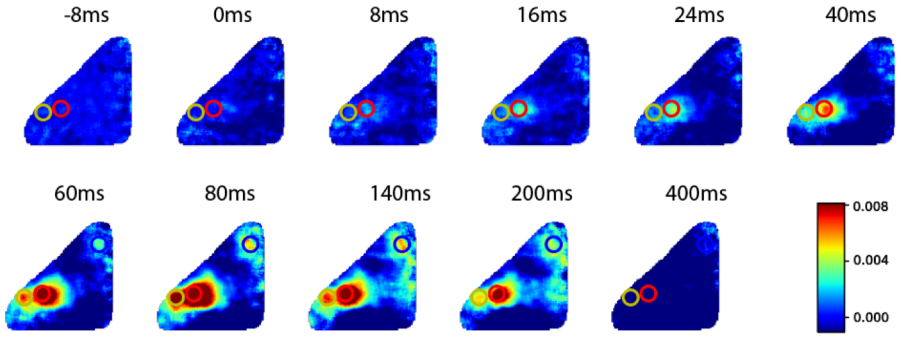
FOV: 6.58 x 6.58 mm

Averaged response n = 20



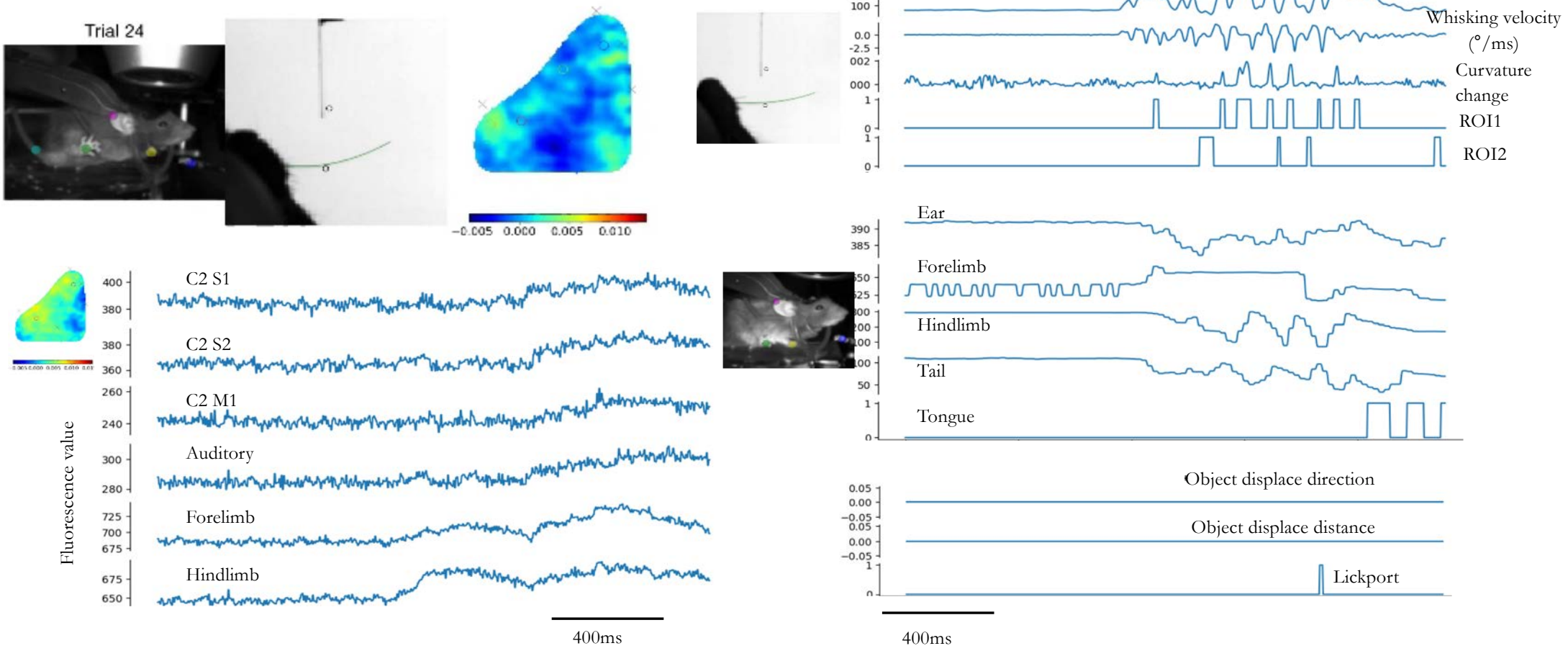
C2 whisker stimulus

GCaMP6f signal



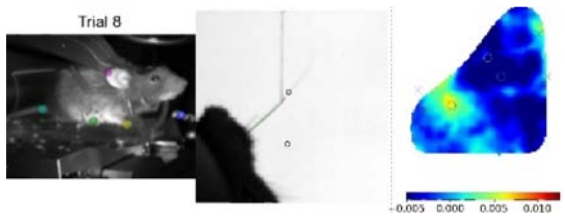
Mouse no .37

Behavioural and Neural data example trial

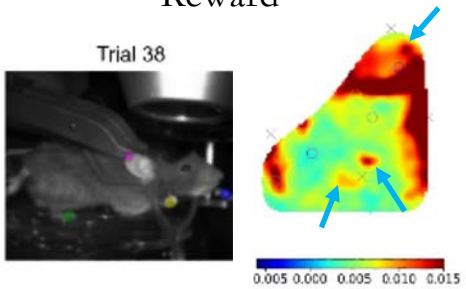


Recurrent motifs of spatiotemporal dynamics

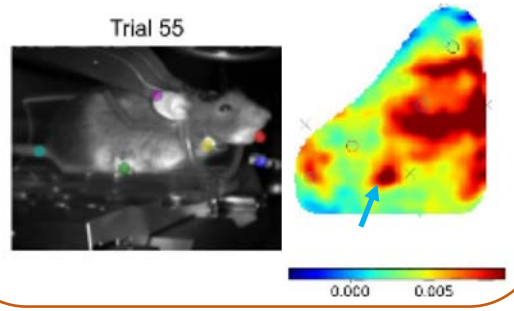
Whisker Touch



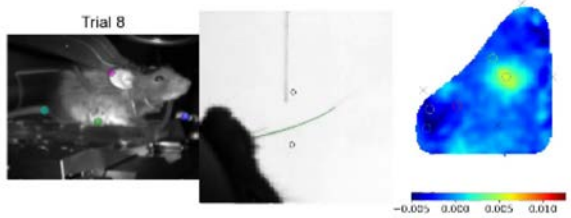
Reward



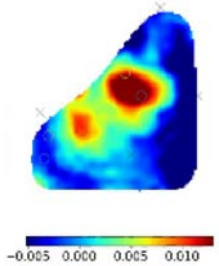
Tongue protraction?



Hindlimb



Forelimb



Focus on touches preceded by large inter-contact intervals (>300 ms)

Conclusion and Summary

- Plasticity linked to the unsupervised learning from natural stimuli might control the late formation of the direction selectivity map in the barrel cortex
- The barrel map, the direction selectivity map and the map for synchronous stimuli are superimposed in the barrel cortex
- A new behavioural task with Reinforcement learning of repeated touches allow to study
    - Change (suppression) of the representation of touch across learning
    - Specific inhibition related to omission events

People - Grants


Yves Kremer


Luc Estebanez


Julien Bertherat


Fan Yang


Romain Brette


Isabelle Férézou


Daniel Shulz


Jean-François Léger

Agence Nationale de la Recherche
ANR

FRANCE-BIOIMAGING

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