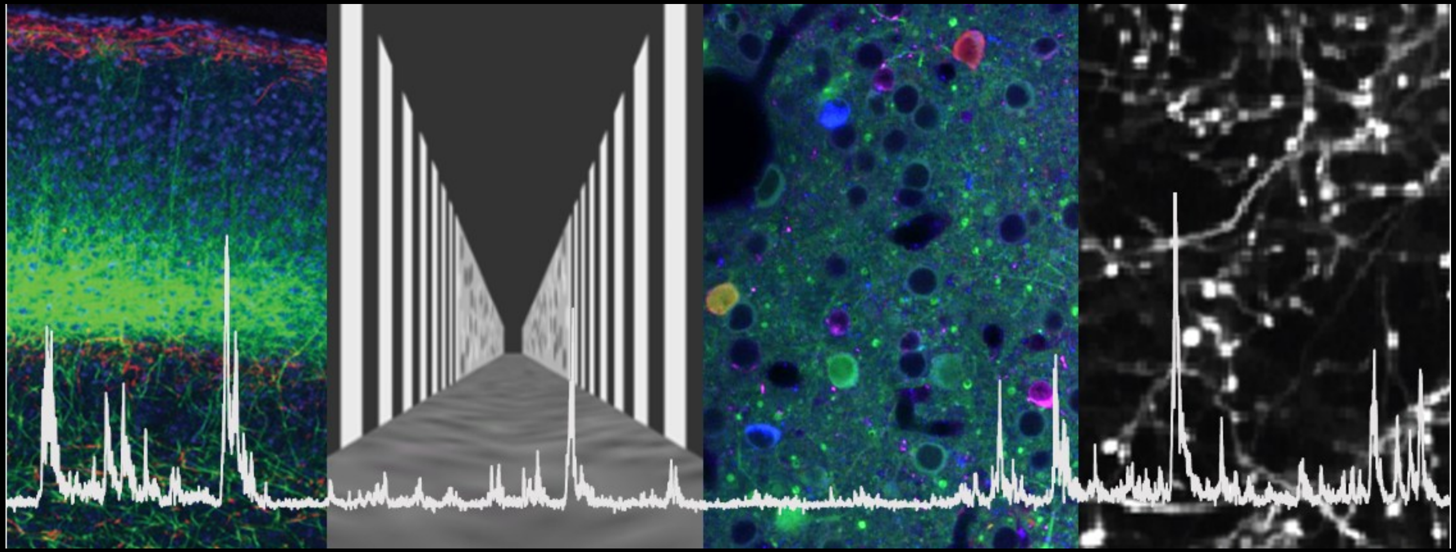
Putting vision into context:

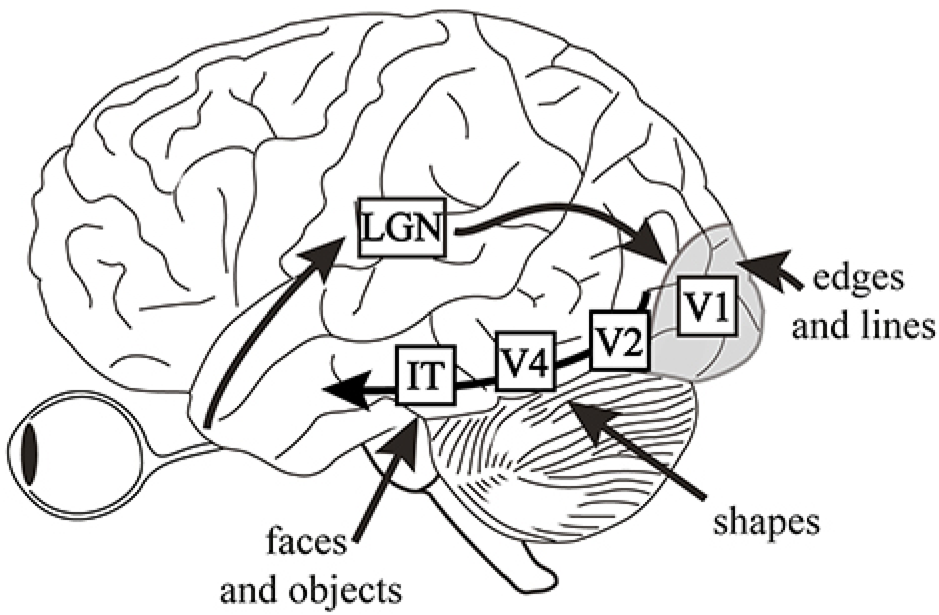
Influence of behaviour and context on sensory processing

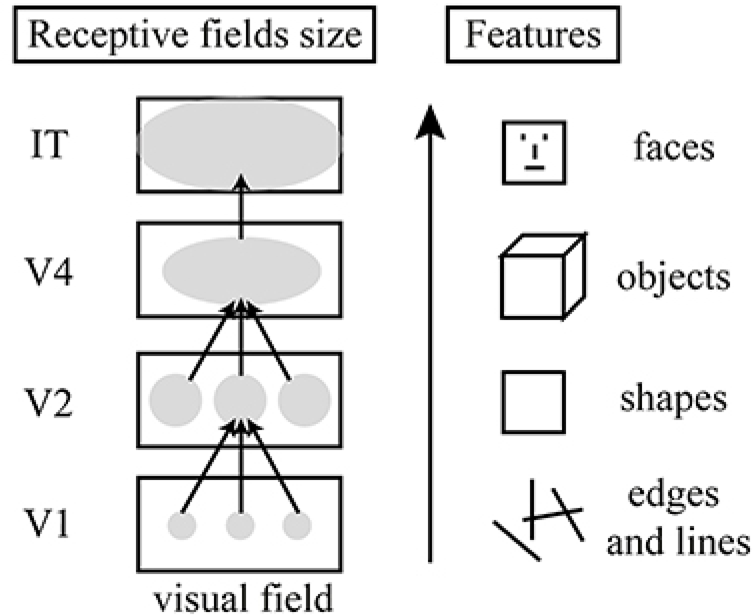


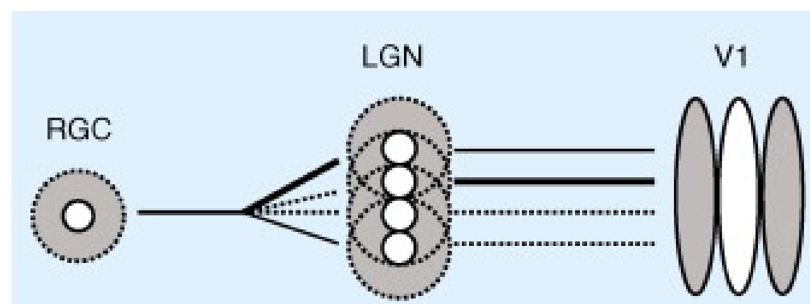
Sonja Hofer

Sensory Systems Module PhD course 22/10/2019

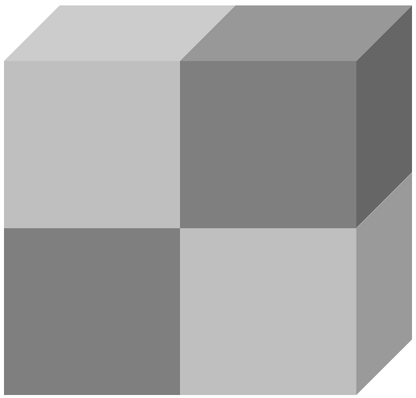
Classical view of hierarchical feed-forward visual processing







Problems with the hierarchical feed-forward model

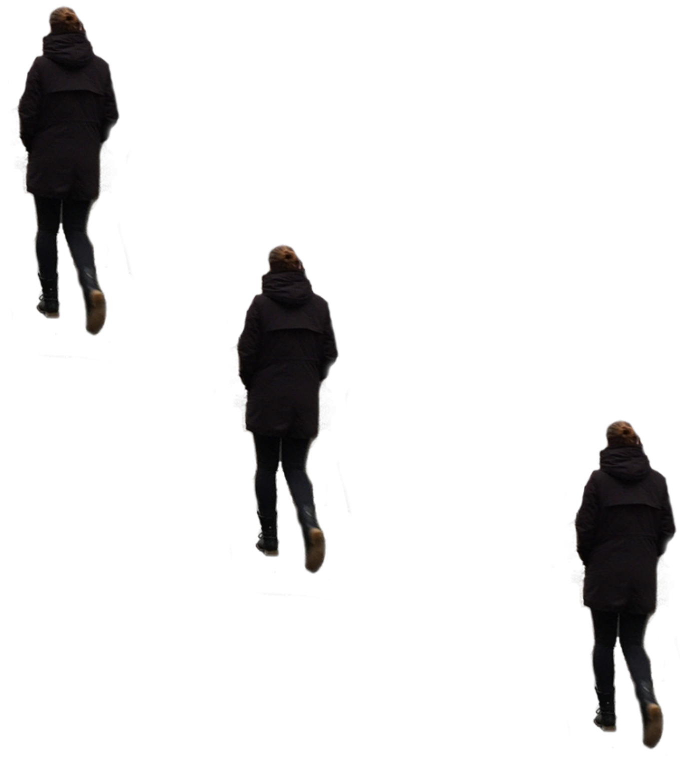


Most properties of the environment cannot be directly deduced from sensory input

Analyzing complex visual scenes requires a model of the world

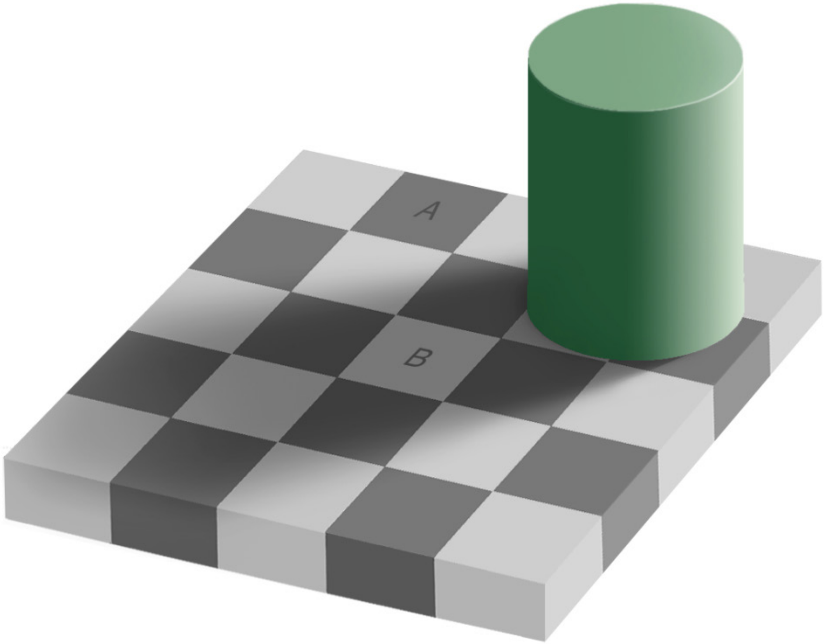
Our model of the world shapes our perception

Our model of the world shapes our perception



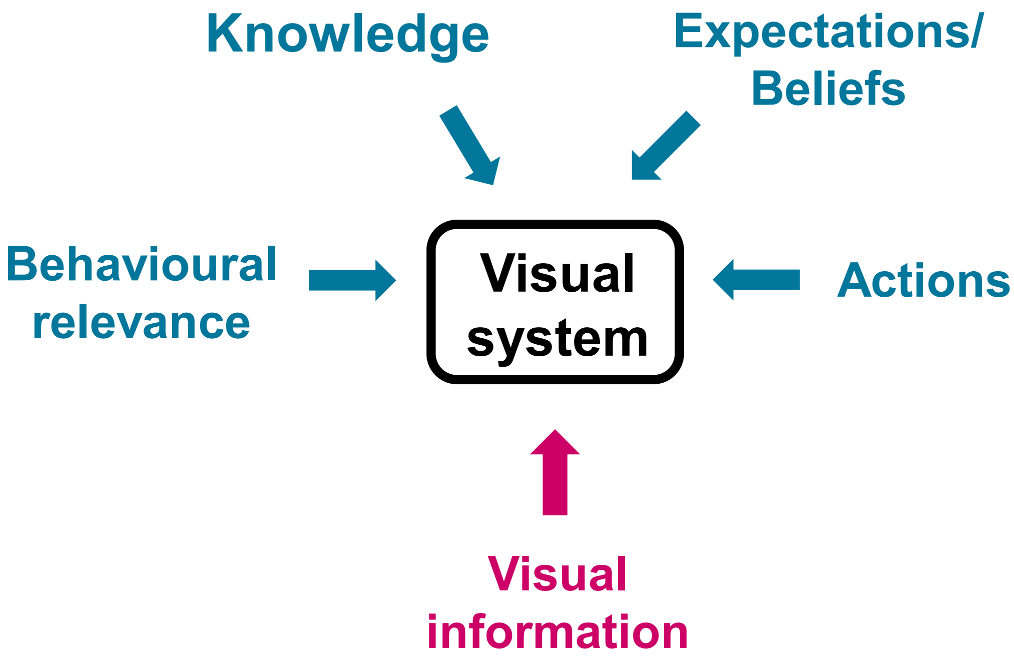
Our model of the world shapes our perception

Effect of context on perception:



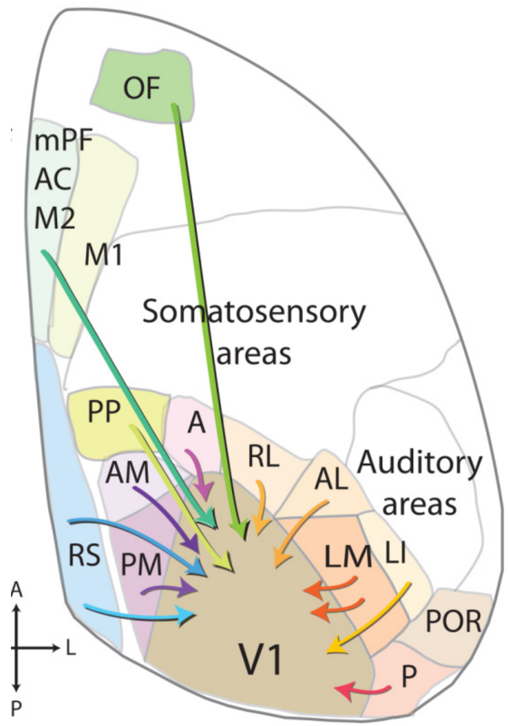
Effect of context on perception:

Integration of sensory and contextual ‘top-down’ signals

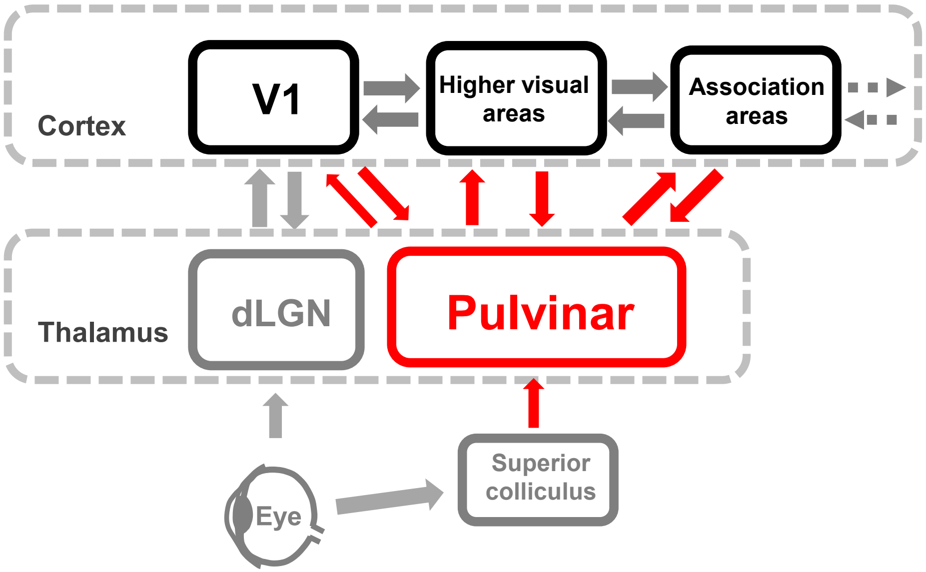


Integration of sensory and contextual ‘top-down’ signals

Top-down cortical inputs



Higher-order thalamic inputs



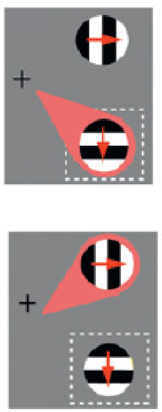
Neuromodulation

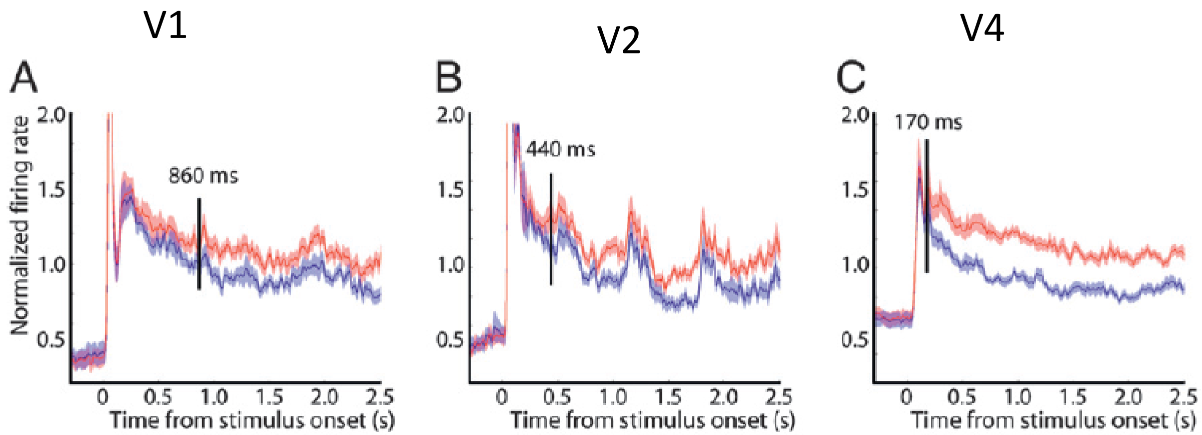
Outline

- Neuronal signals related to attention and reward expectation
- Behavioural relevance & Learning
- Motor signals in sensory cortex
- Bayesian inference and predictive coding

Modulation of sensory responses by attention

Spatial attention (Top-down)



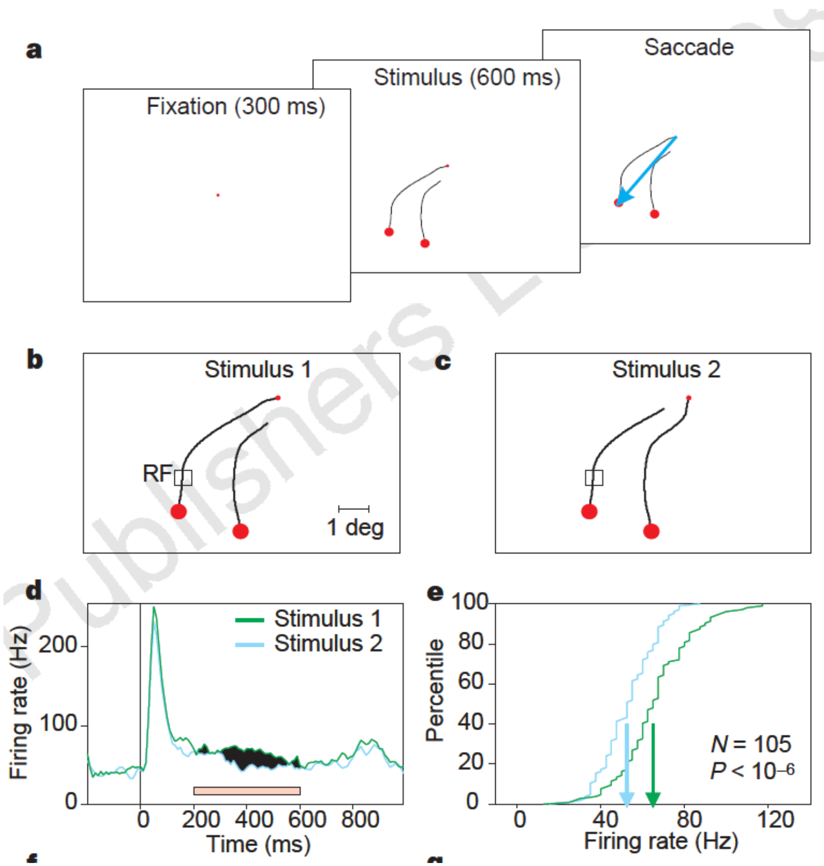


Buffalo et al 2009

Modulation of sensory responses by attention

Object-based attention

Curve-tracing task

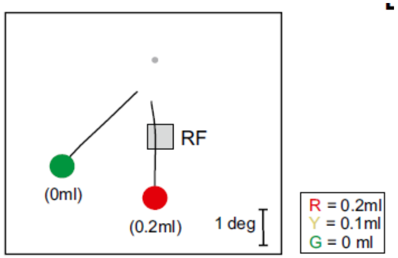


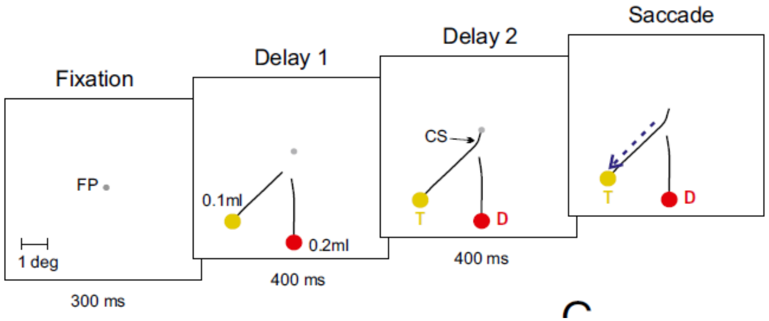
Roelfsema et al 1998

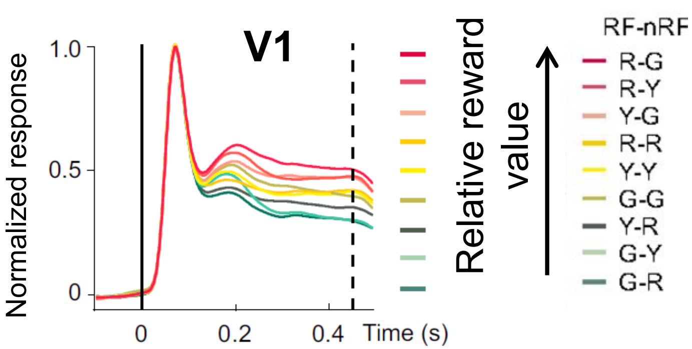
Modulation of sensory responses by reward expectation

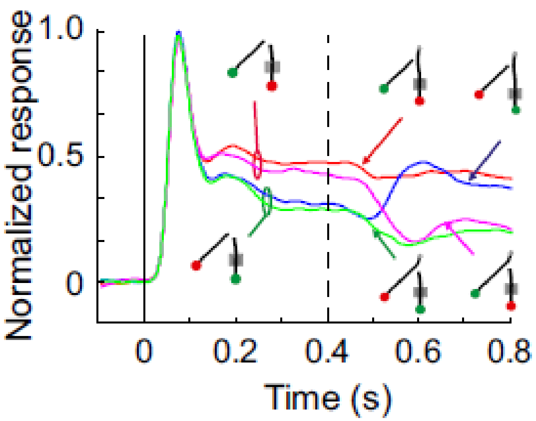
Attention or reward expectation?

Adapted curve-tracing task









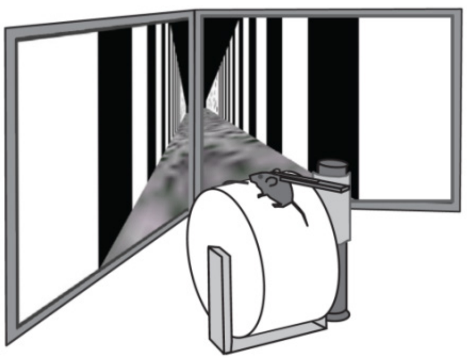
Stănişor et al, 2013

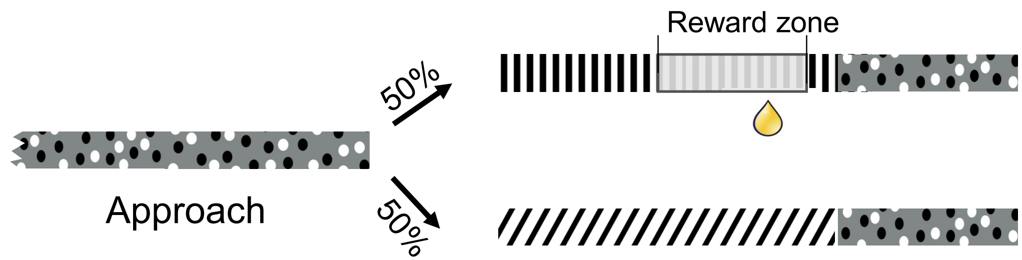
Changes of sensory responses during learning

How do responses to visual stimuli change as they become behaviourally relevant to an animal?

Changes of sensory responses during learning

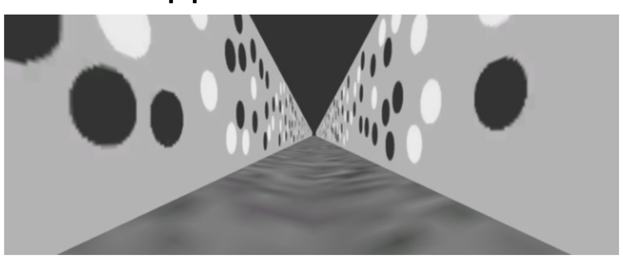
Visual discrimination task in virtual reality

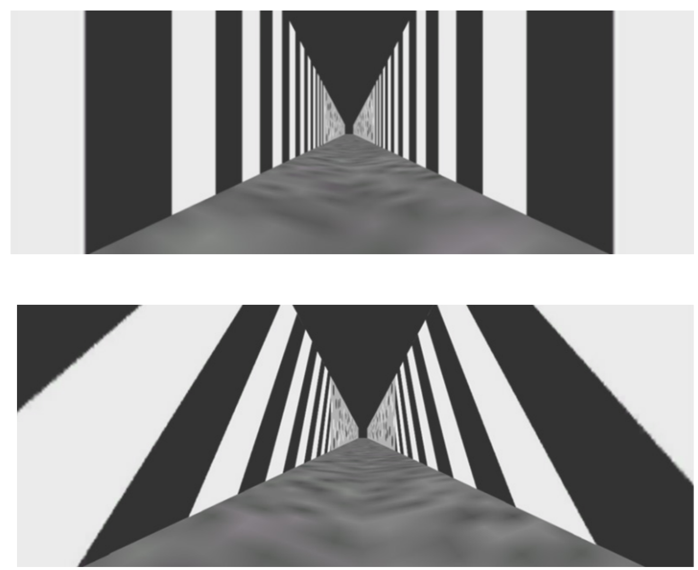




Grating corridors

Approach corridor





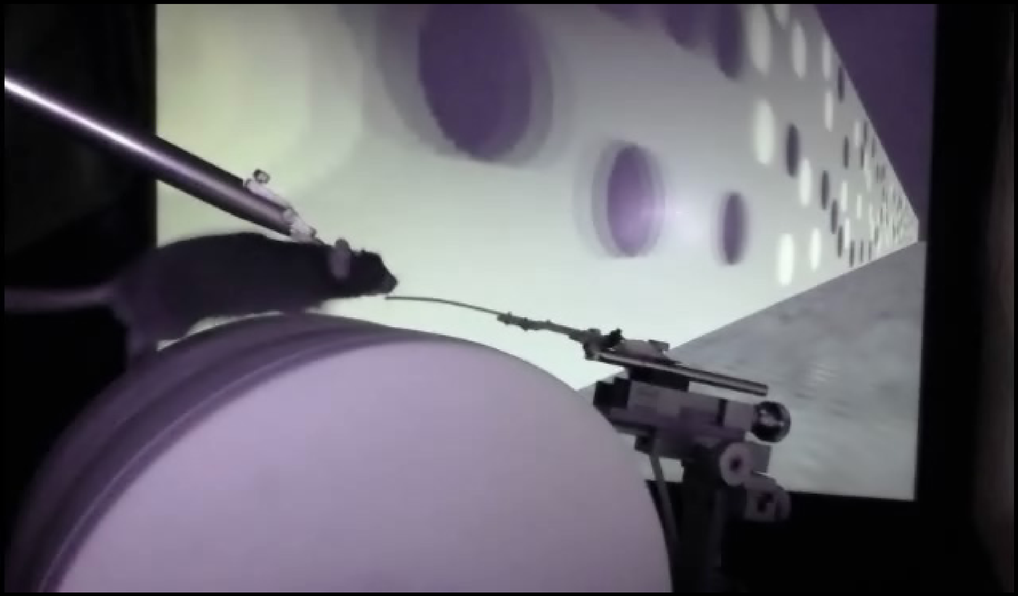
Vertical: rewarded
(drop of soya milk)

Angled (40°): non-rewarded

Adil Khan

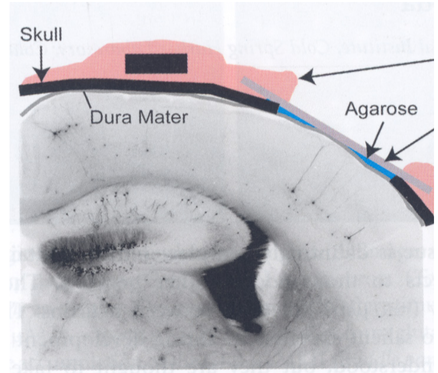
Trained mouse performing the task

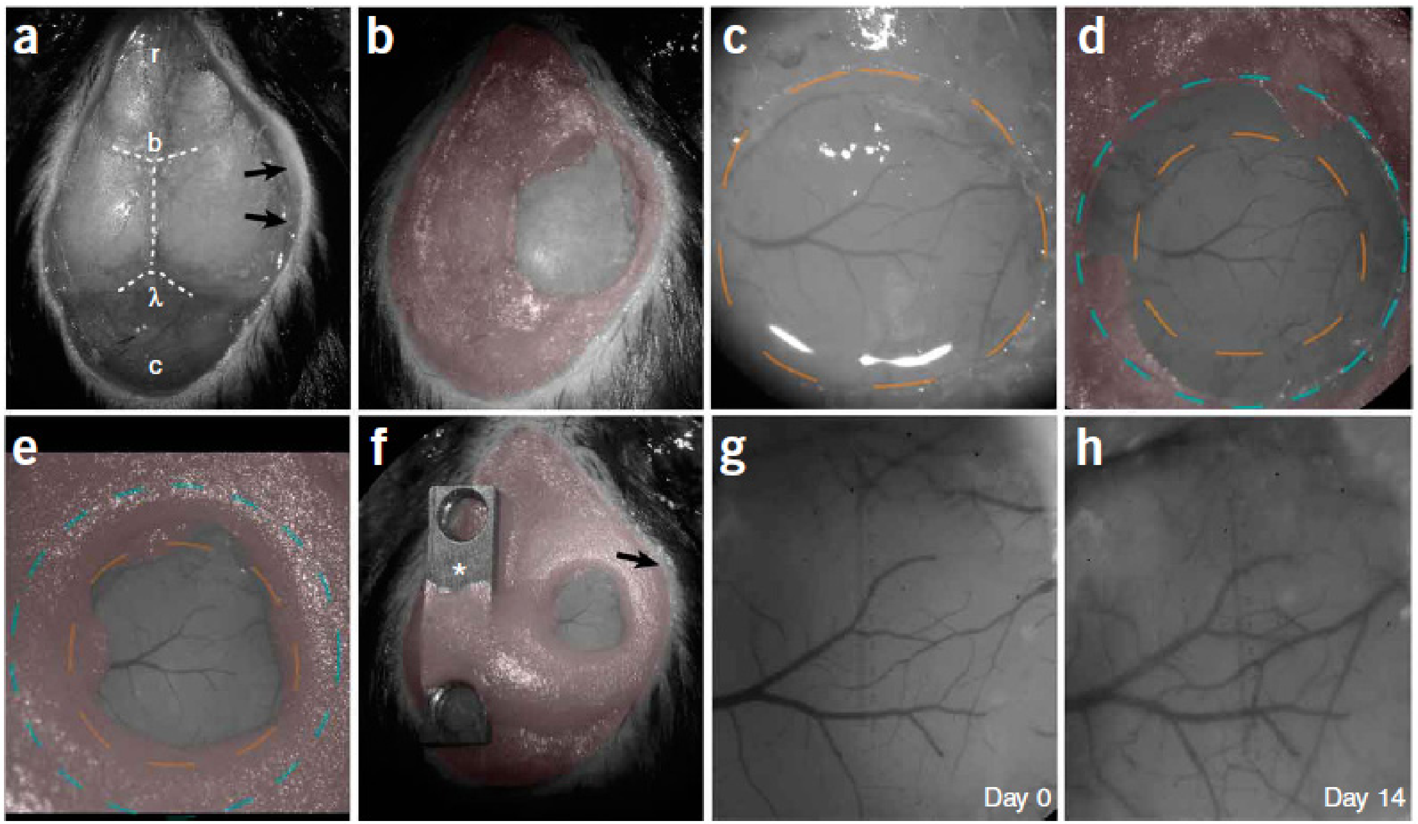
Head-fixed mouse on a cylinder,
running through a virtual corridor
(only half of virtual reality visible)



Access to the cortex for chronic recordings

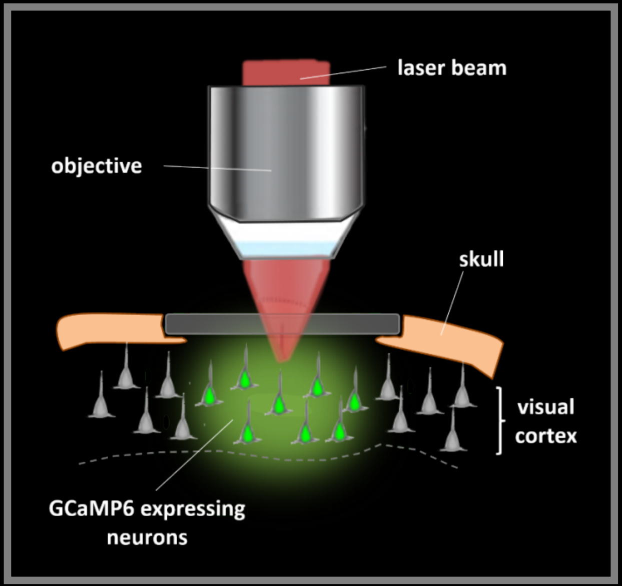
Implantation of a chronic cranial window:



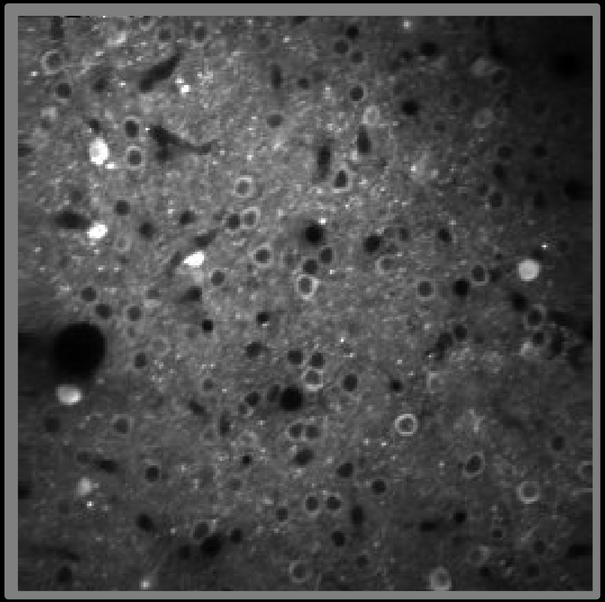


Holtmaat et al., 2009

Two-photon calcium imaging of GCaMP calcium indicators



GCaMP6-expressing neurons in visual cortex (V1)

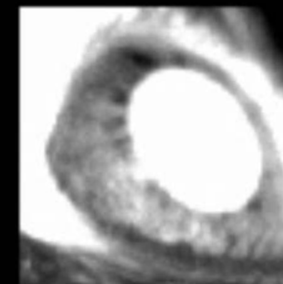


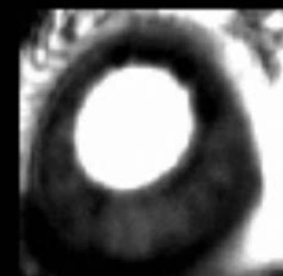
In vivo two-photon calcium imaging during the discrimination task

Trained mouse performing the task

Neurons in visual cortex expressing GCaMP6

Eye position

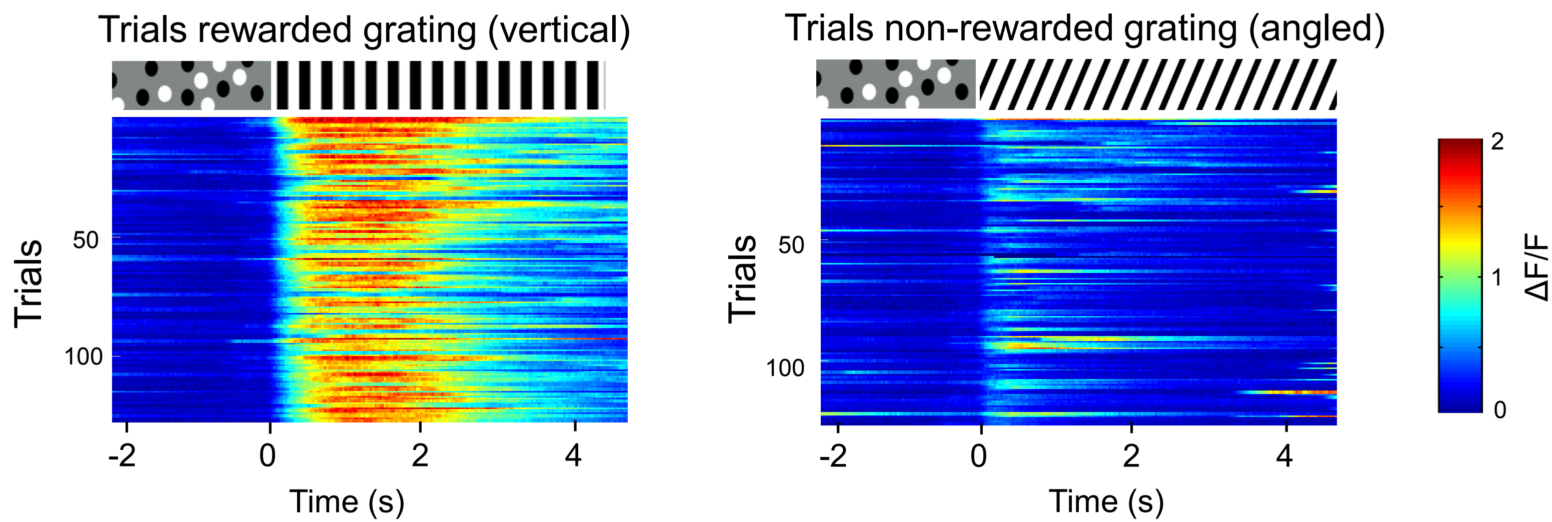




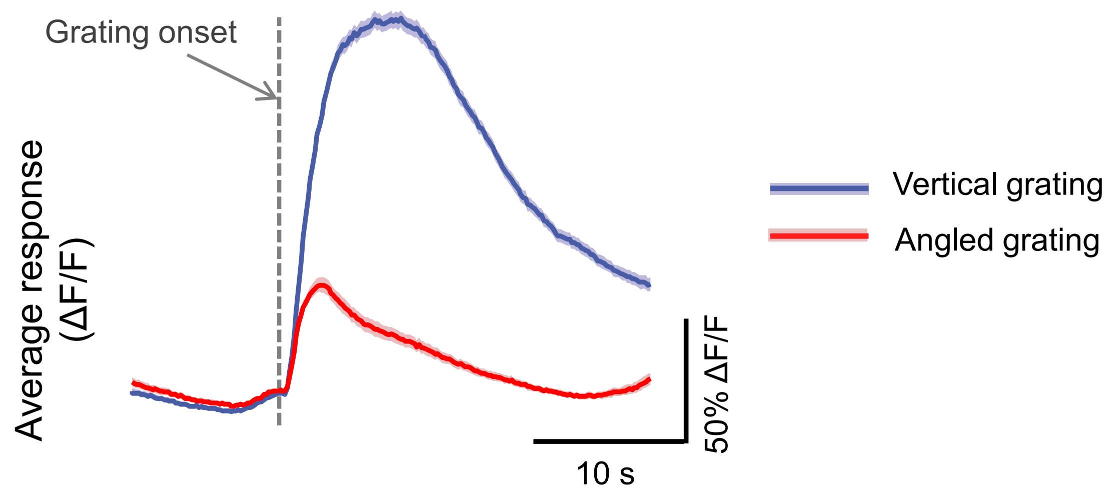
Speed 2.5x

Neuronal responses to task-relevant stimuli

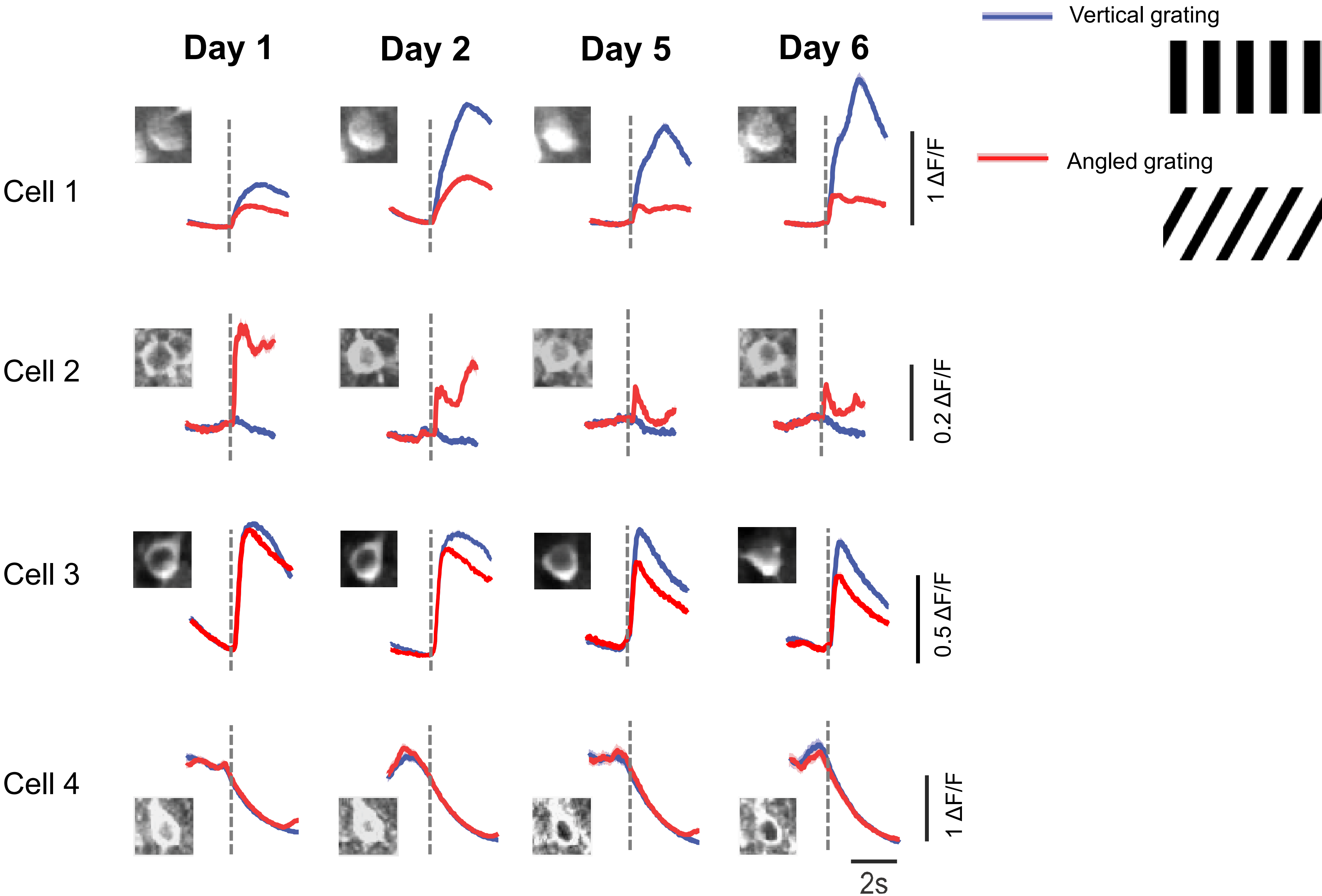
Example cell response to grating corridors:



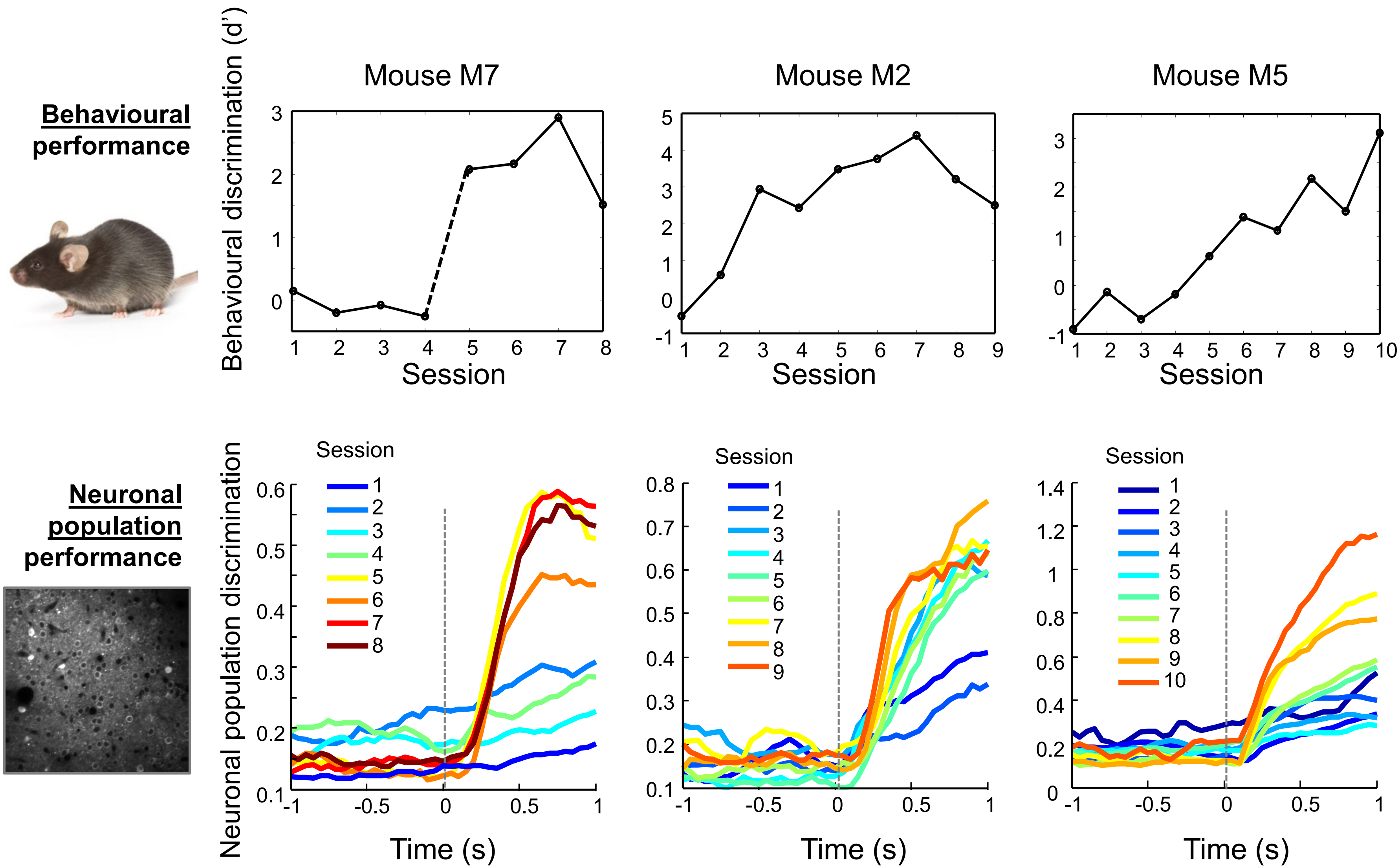
Average response



Neuronal responses to task-relevant stimuli

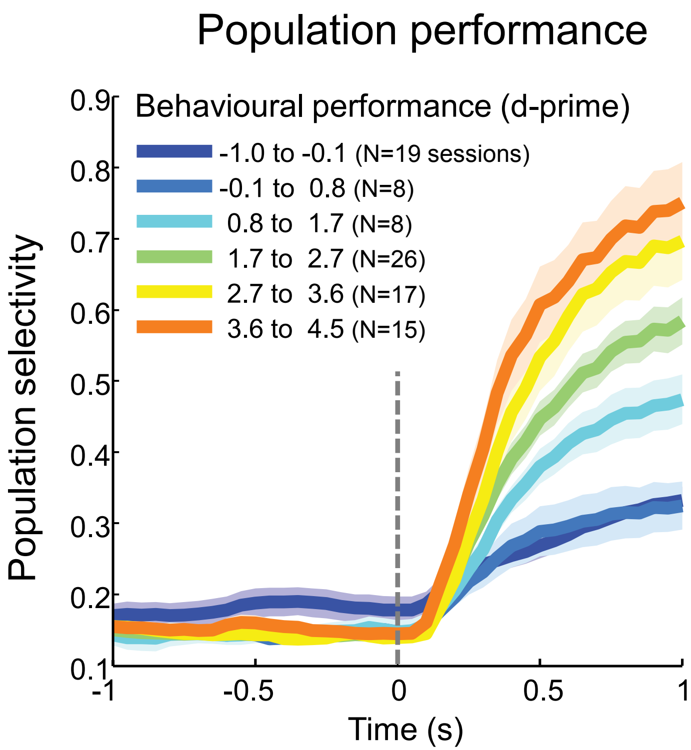


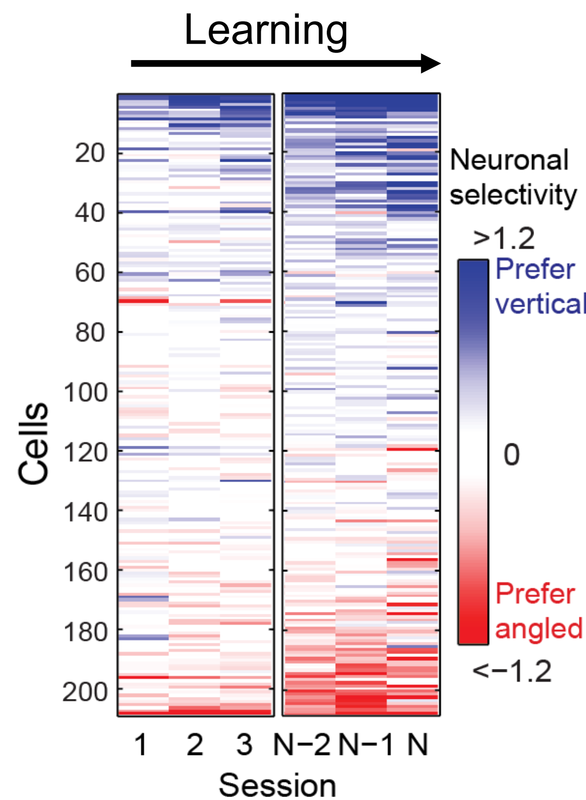
Relationship between behavioural and neuronal performance



Poort, Khan et al., Neuron 2015

Neuronal changes with learning



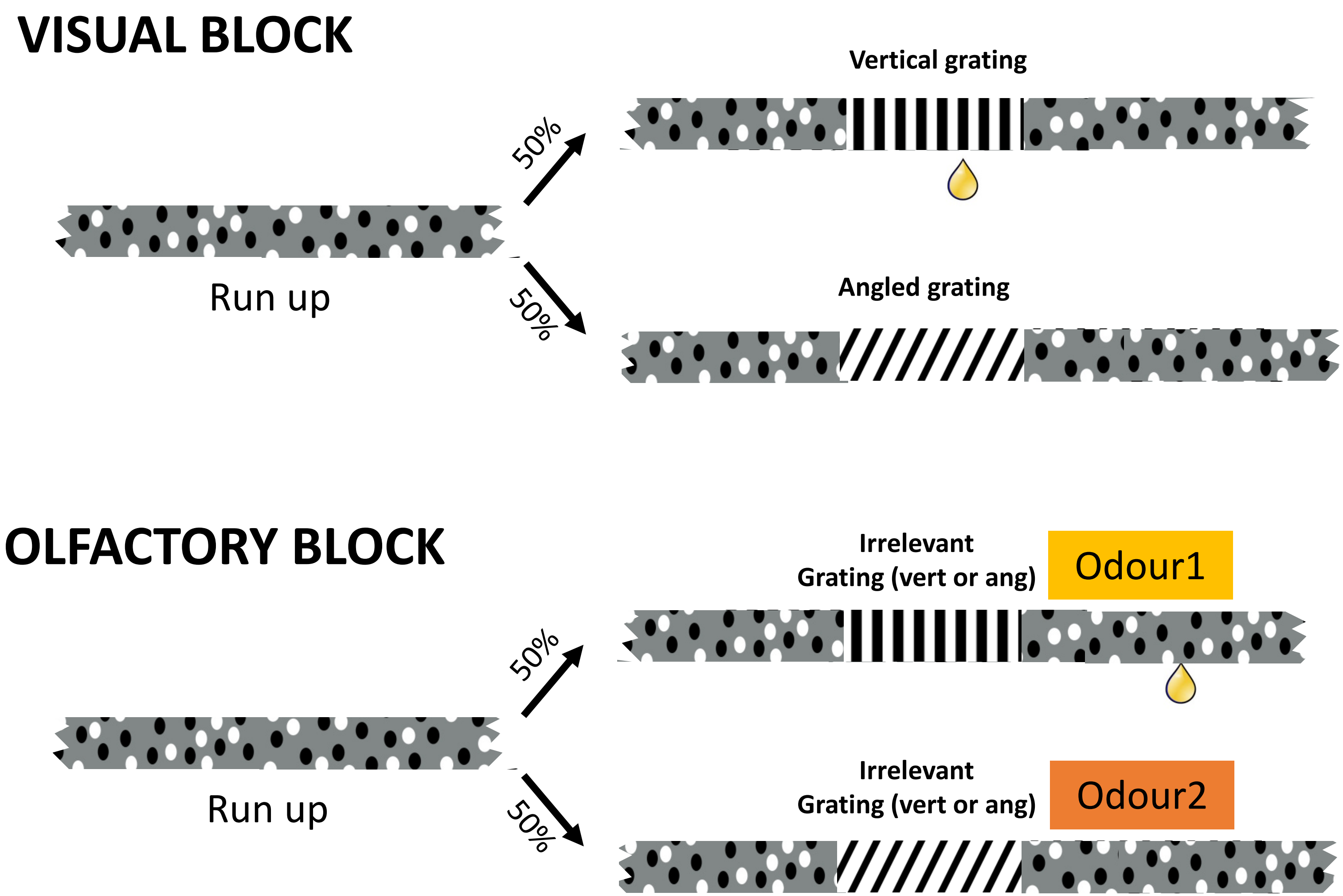


→ **The visual cortex gets better at distinguishing the two task-relevant stimuli, tightly correlated with behavioural performance**

Learning may increase the salience of task-relevant visual information to better inform behavioural decisions

Poort, Khan et al., Neuron 2015

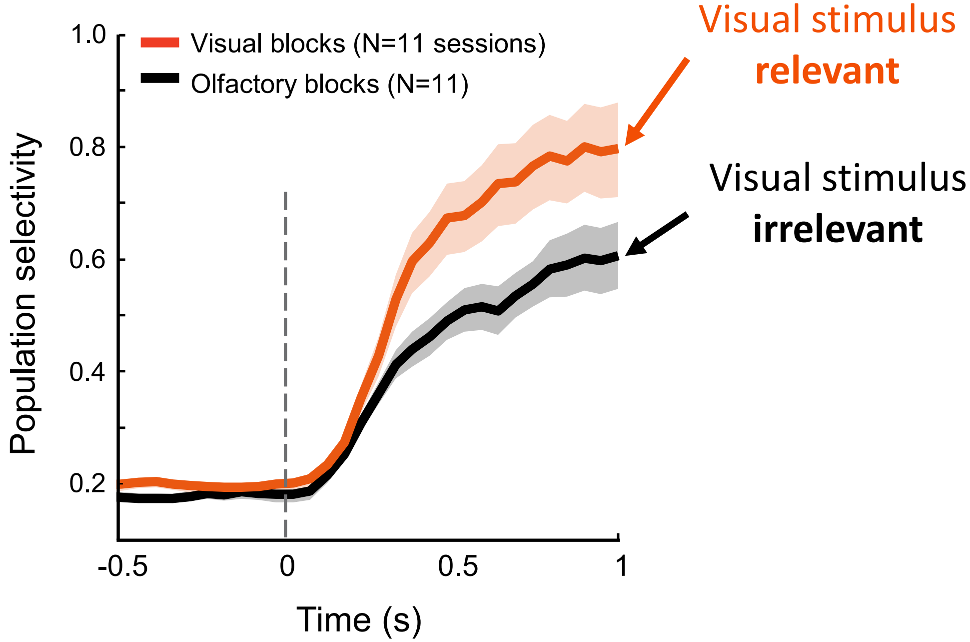
Switching between visual and olfactory discrimination task



Switching between visual and olfactory discrimination task

Mice switch between a visual and an olfactory task
(the same visual stimuli are shown but ignored)

Population discriminability

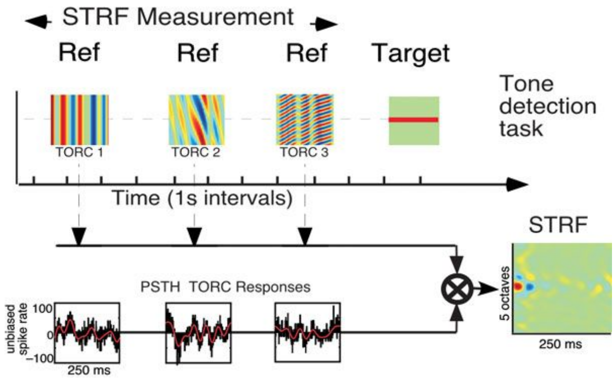


→ **Neurons in V1 are more selective when visual stimuli are relevant**

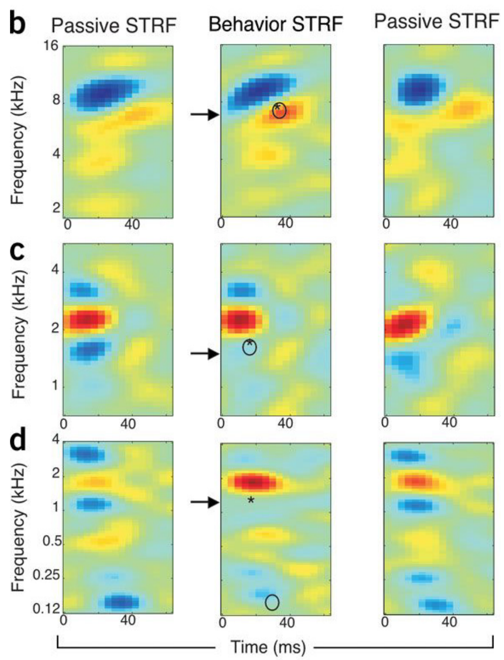
Poort, Khan et al., Neuron 2015

Modulation of sensory responses by task demands

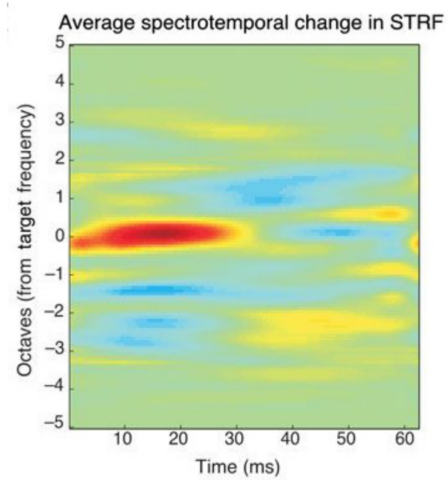
Task-dependent changes in auditory cortex receptive fields



STRF: spectrotemporal response field



Average change in response field passive listening vs during task

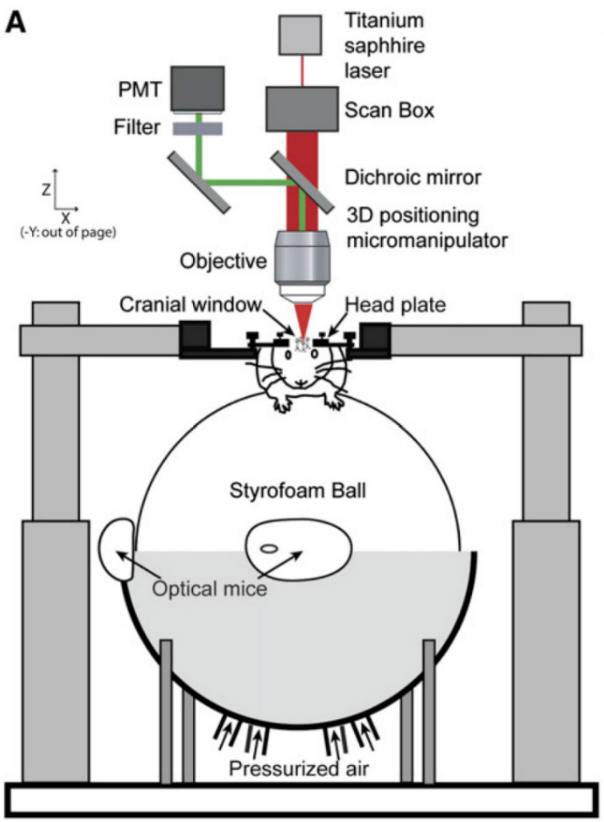


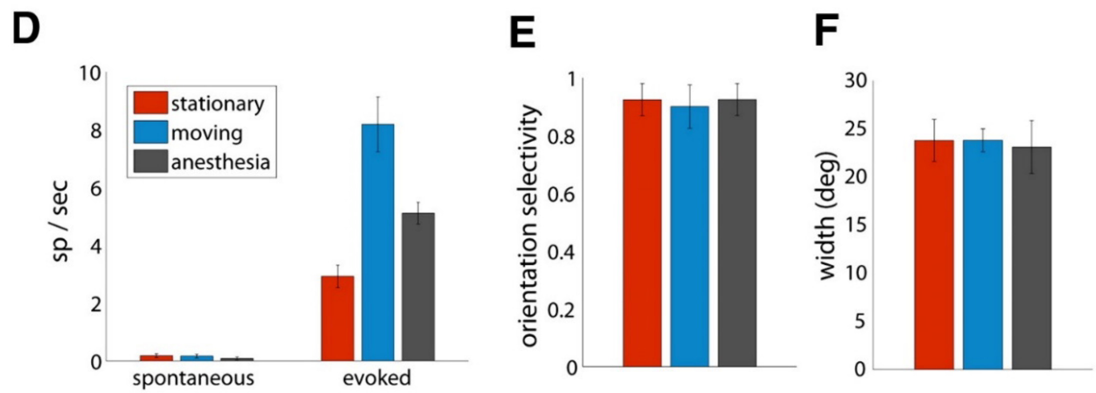
Sensory response properties are not fixed but reflect behavioural demands!

Fritz et al, 2003

Motor signals in sensory areas

Electrophysiological recordings in primary visual cortex in head-fixed, running mice



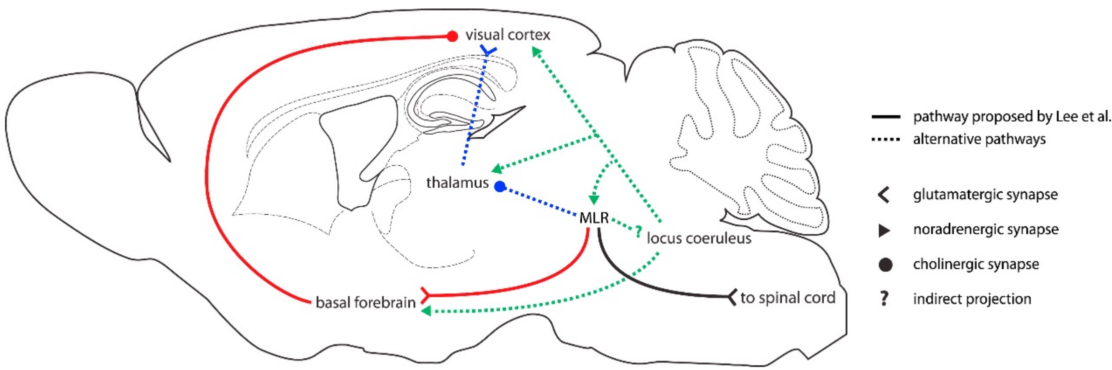


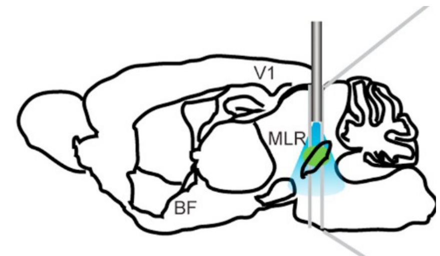
Visual responses in V1 are increased during locomotion

Niell & Styker, 2010

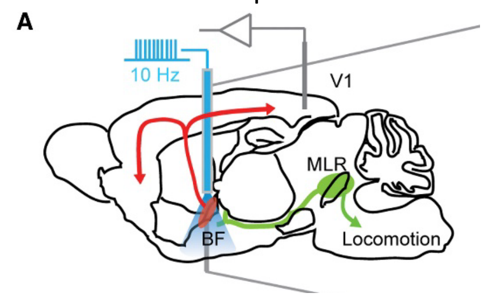
Motor signals in sensory areas

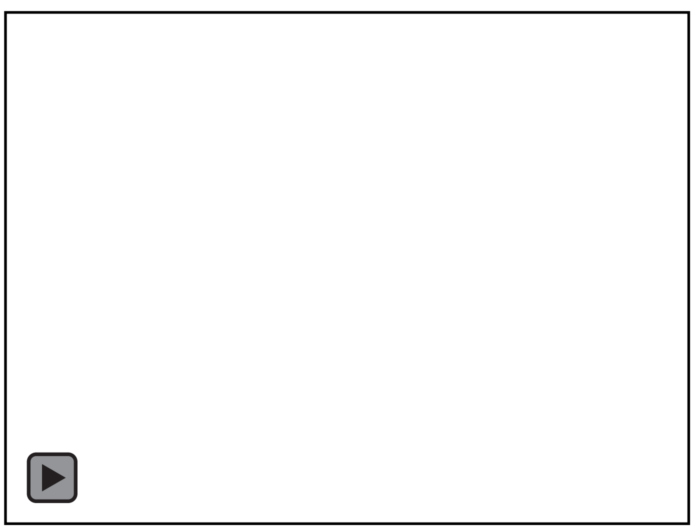
Circuit-mechanisms of locomotion-related signals in visual cortex?

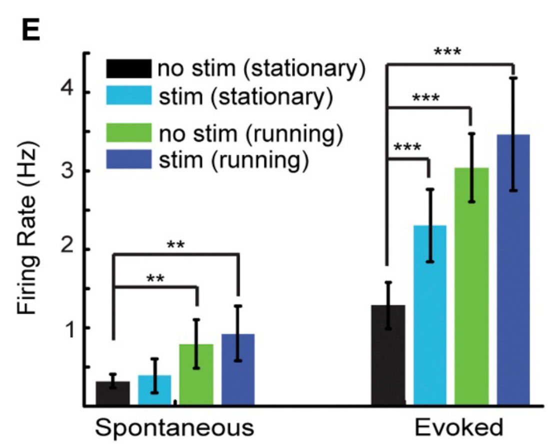




MLR: mesencephalic locomotor region



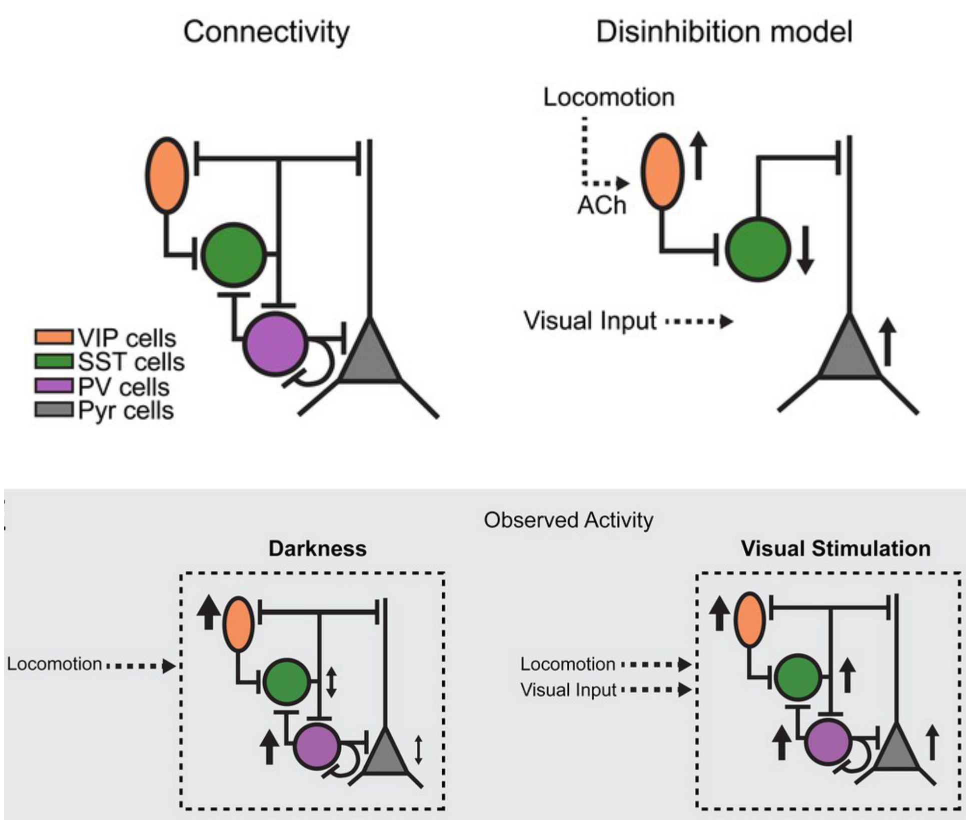


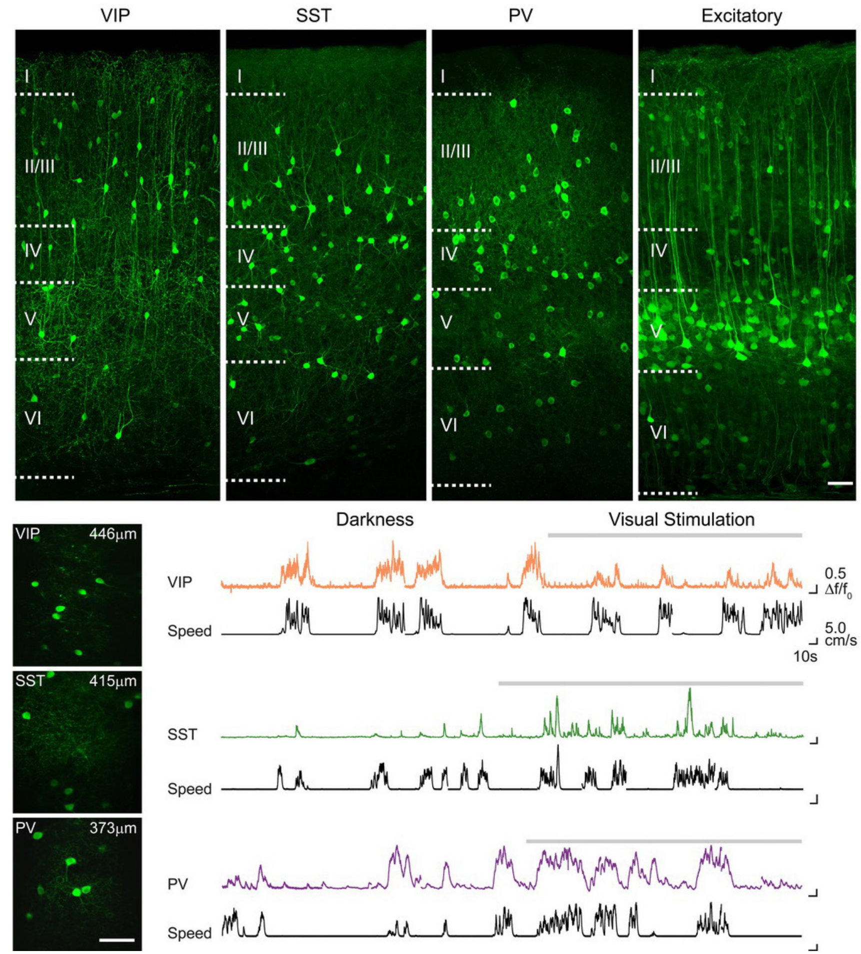


Lee at al., 2014

Motor signals in sensory areas

Circuit-mechanisms of locomotion-related signals in visual cortex?





Complex networks!! -> Modelling

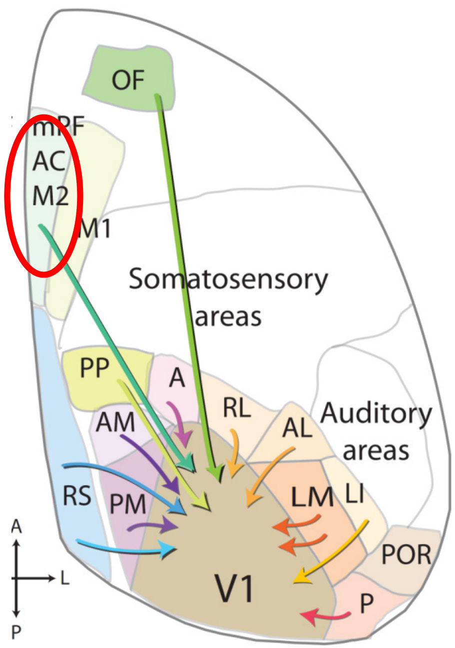
Del Molino at al., 2017

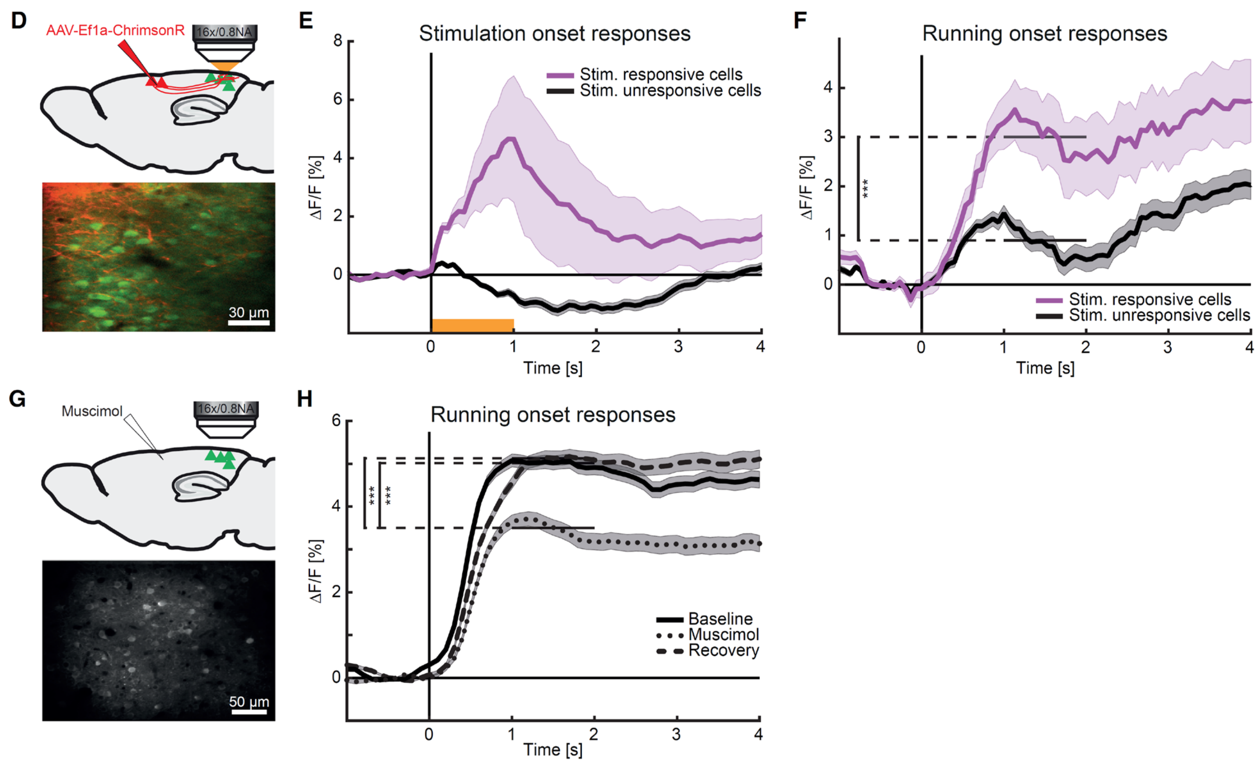
Fu at al., 2014
Pakan at al., 2016

Motor signals in sensory areas

Origin of motor signals?

Anterior cingulate cortex (+ secondary motor cortex)?



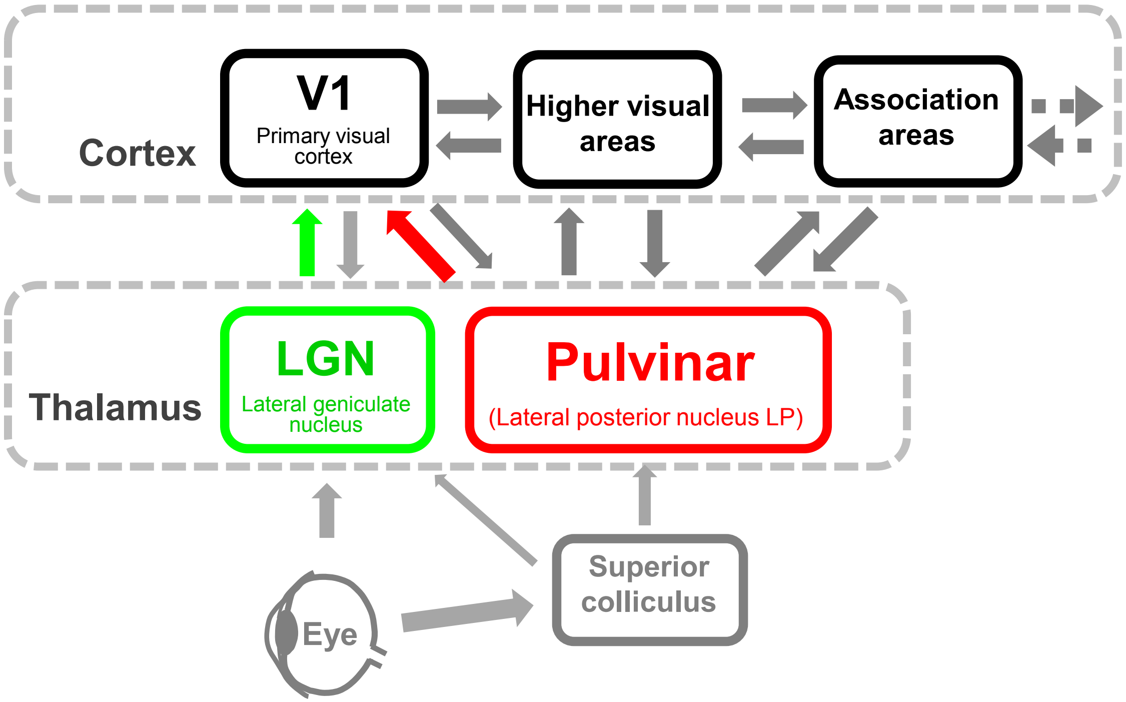


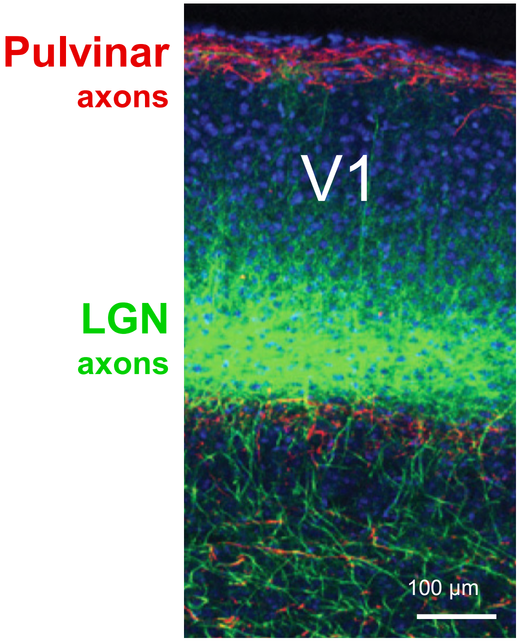
Leinweber at al., 2017

Motor signals in sensory areas

Origin of motor signals?

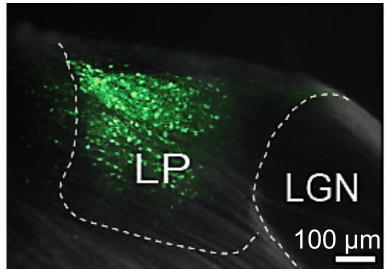
Thalamus?

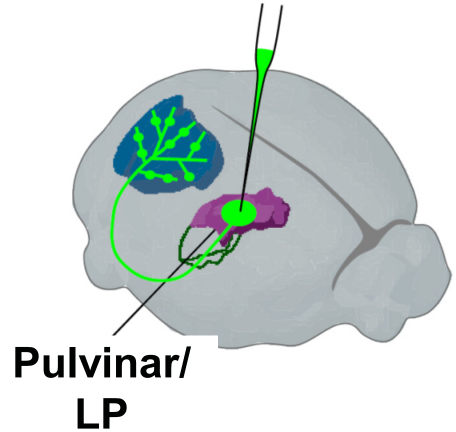




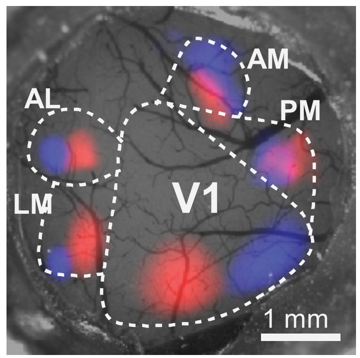
Imaging activity of thalamic projections in cortical areas

Expression of calcium indicator in pulvinar or LGN



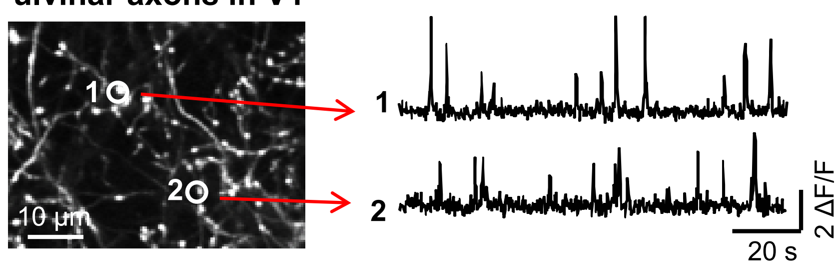


Intrinsic signal imaging to determine position of visual areas

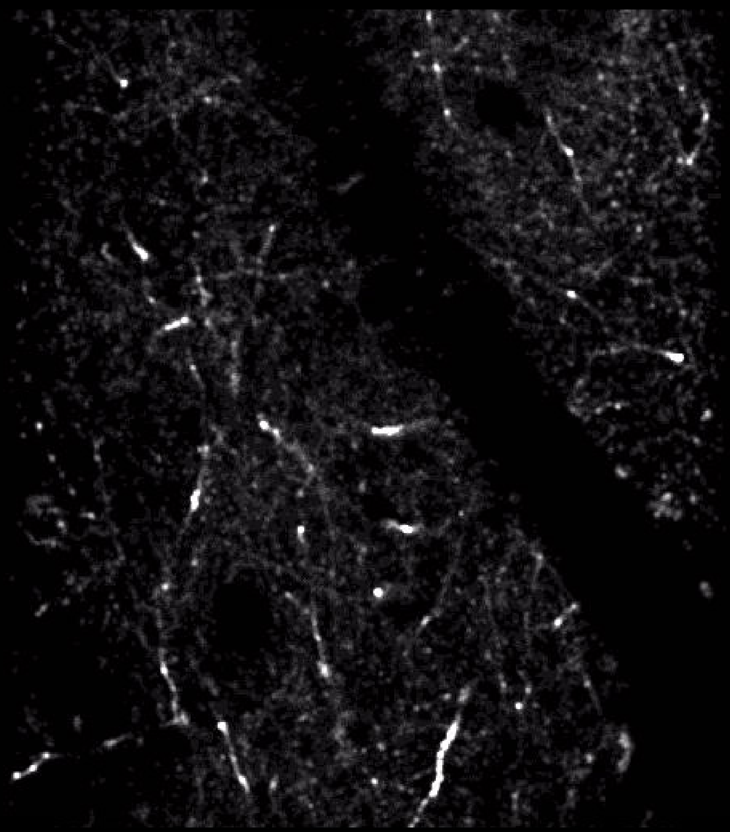


Two-photon imaging of thalamic projections in V1

Pulvinar axons in V1



In vivo two-photon calcium imaging of thalamic axons and boutons in layer 1 of V1

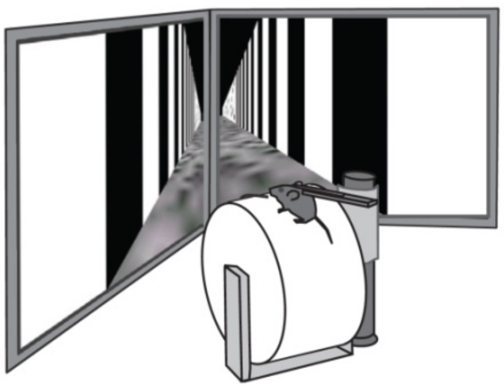


Speed 5x

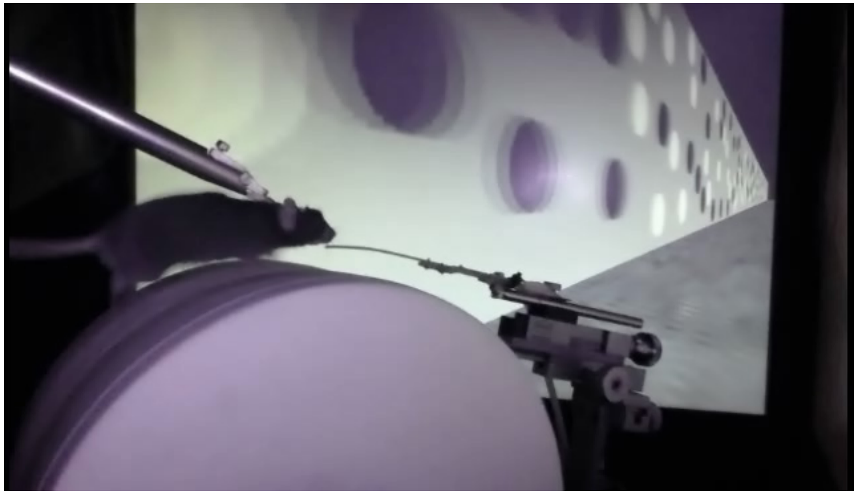
15 µm

Imaging activity of thalamic projections in V1

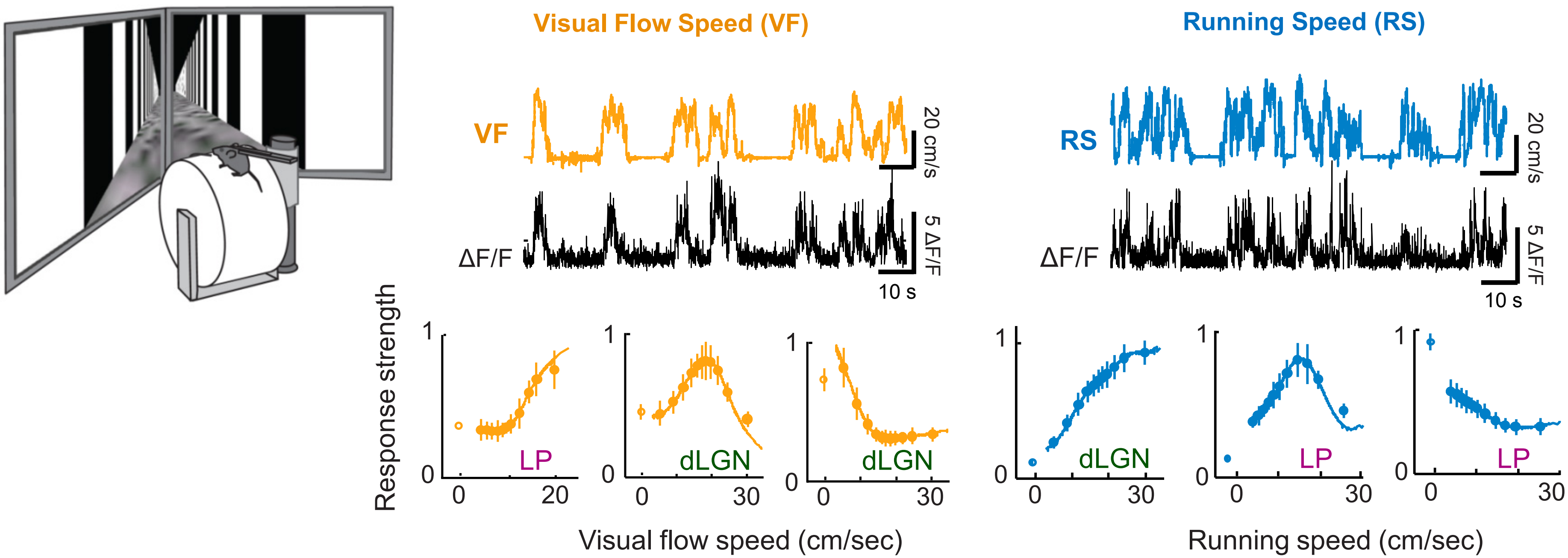
Visuo-motor ‘task’

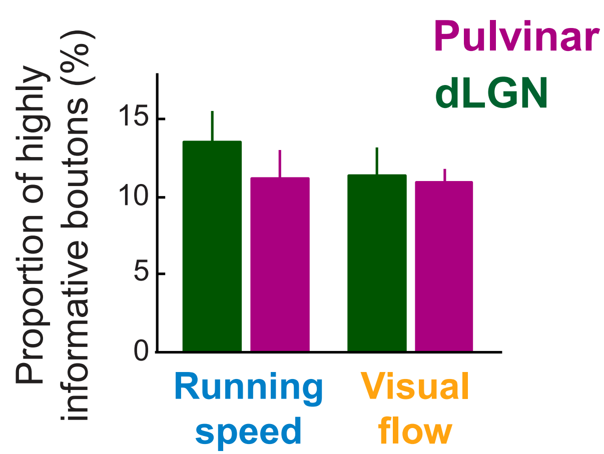


- Trained to run through virtual corridor
- Running uncoupled from visual flow



Visuo-motor signals in thalamic boutons in V1



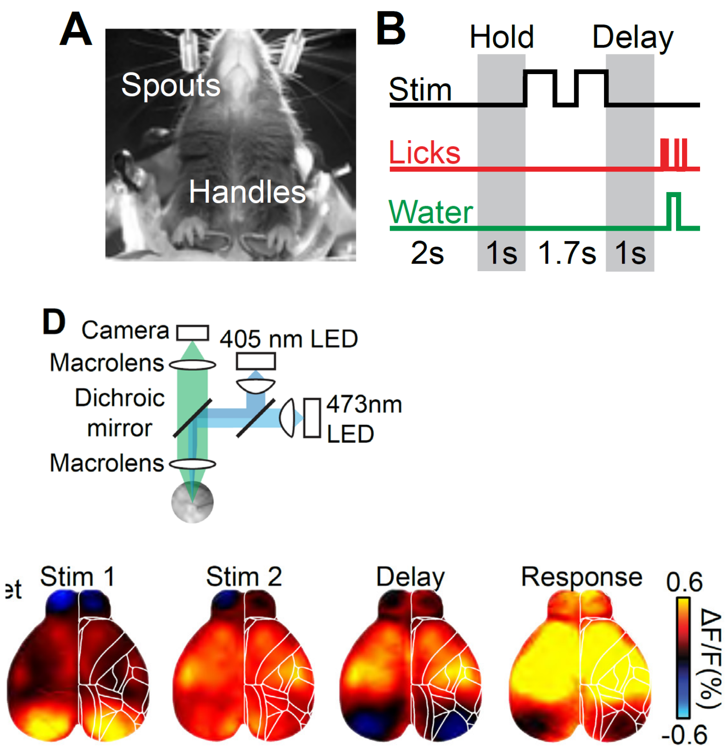


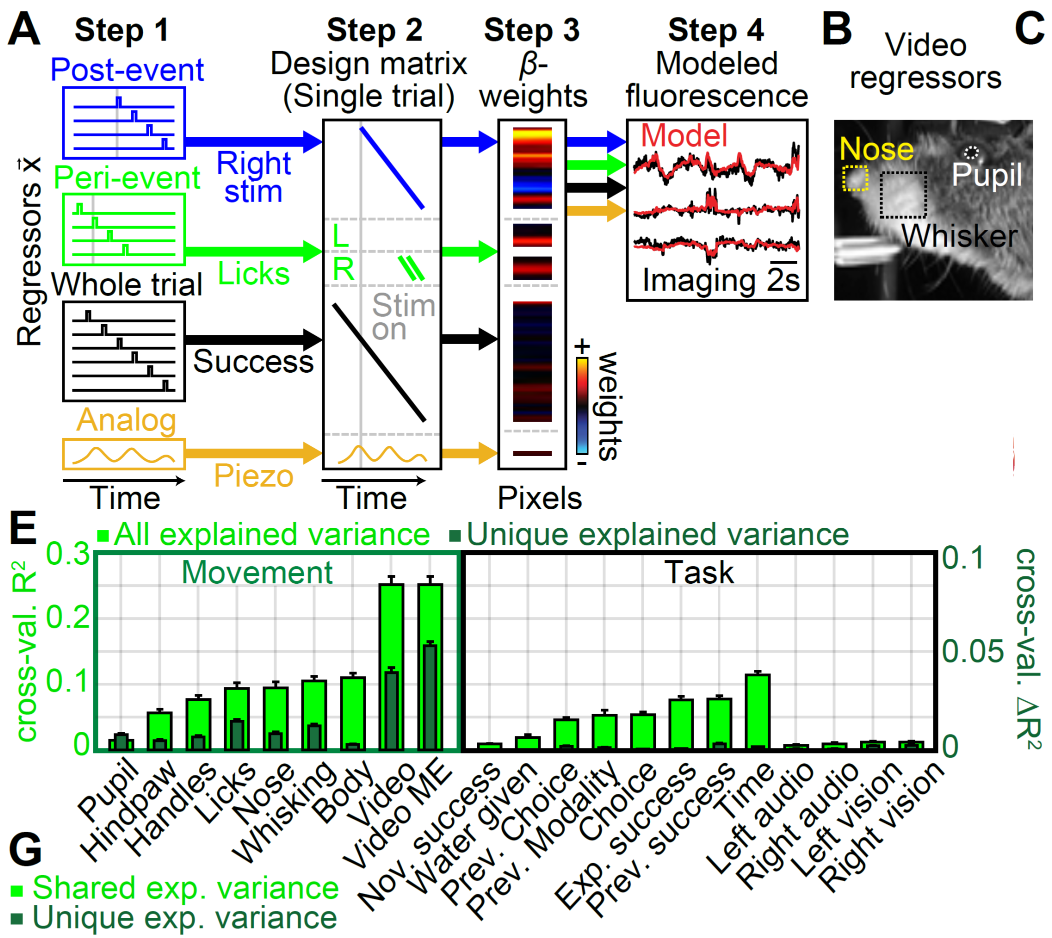
Roth, Dahmen, Muir et al.,
Nature Neurosciene 2016

Motor signals in sensory areas

Motor signals seem to dominate neuronal activity across the cortical surface

Widefield calcium imaging of cortical activity during a simple spatial discrimination task



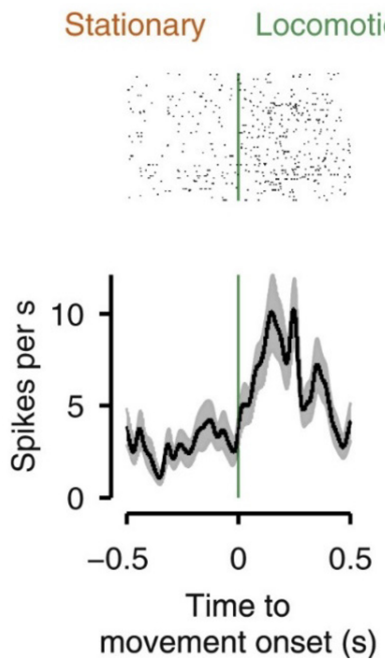


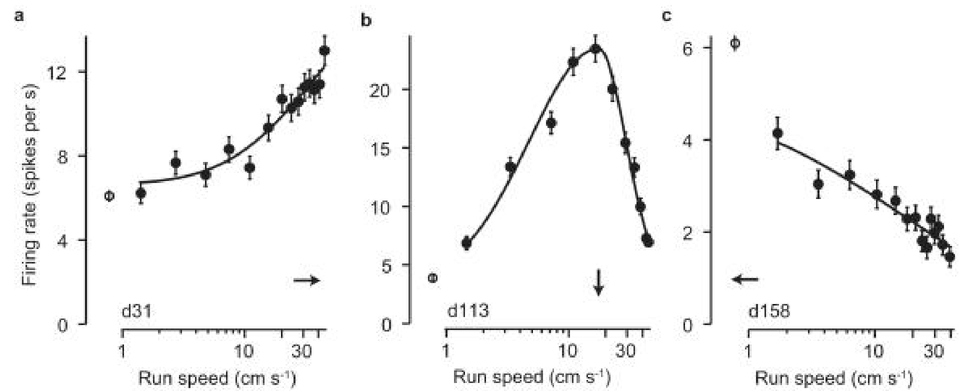
Musall at al., bioRxiv 2018

Motor signals in sensory areas

Just gain control? No!

Activity in visual cortex excitatory cells:
modulated in the dark and carry detailed running speed information



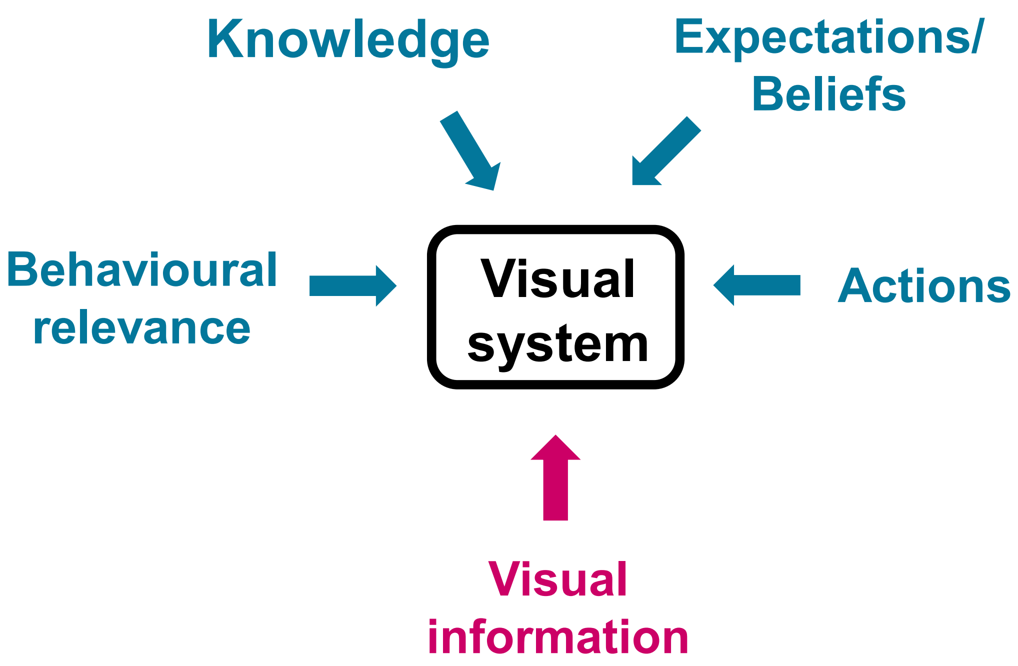


Erisken at al., 2014
Saleem at al., 2013

Motor signals in sensory areas

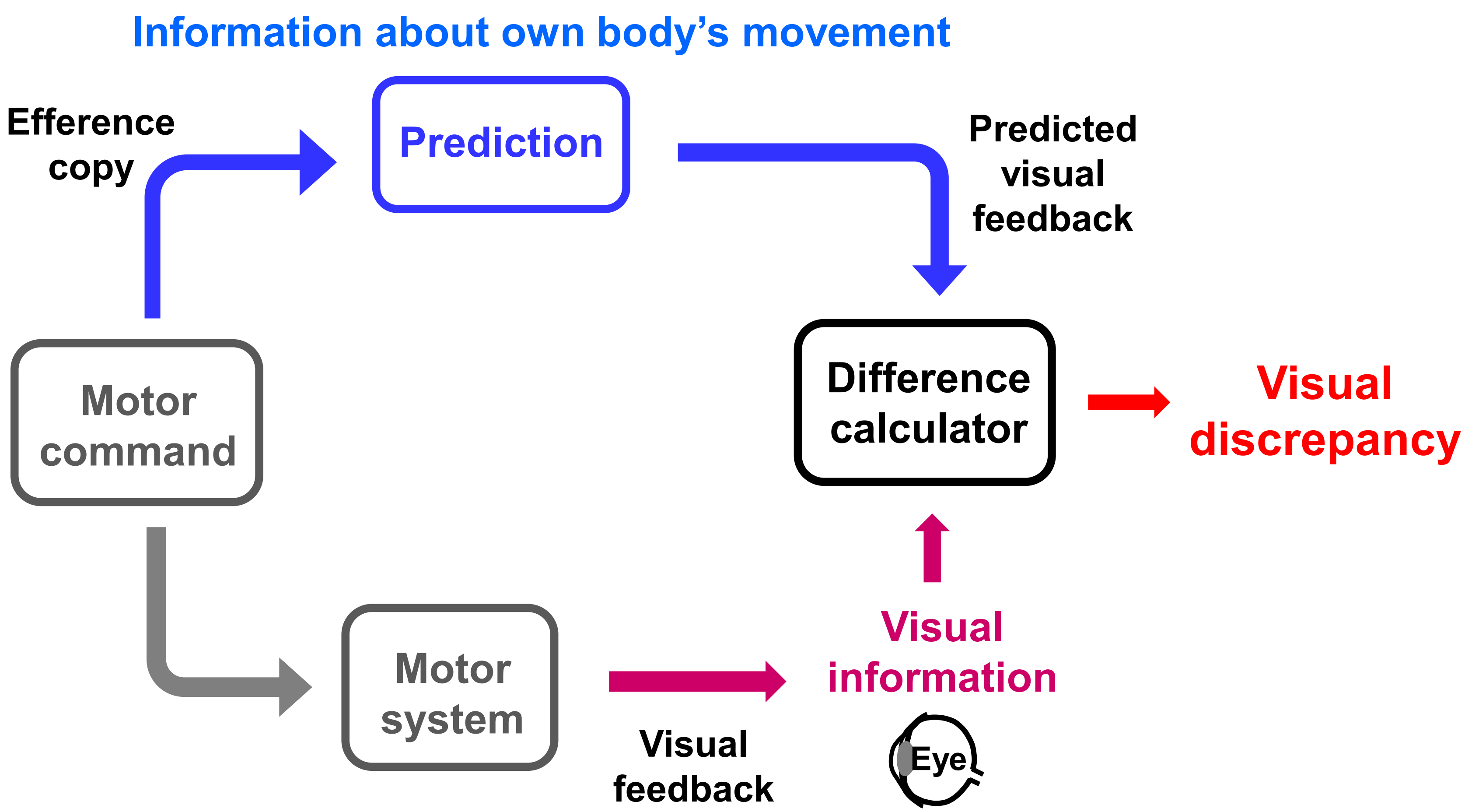
Motor signals as efference copy?

Integration of sensory and contextual ‘top-down’ signals

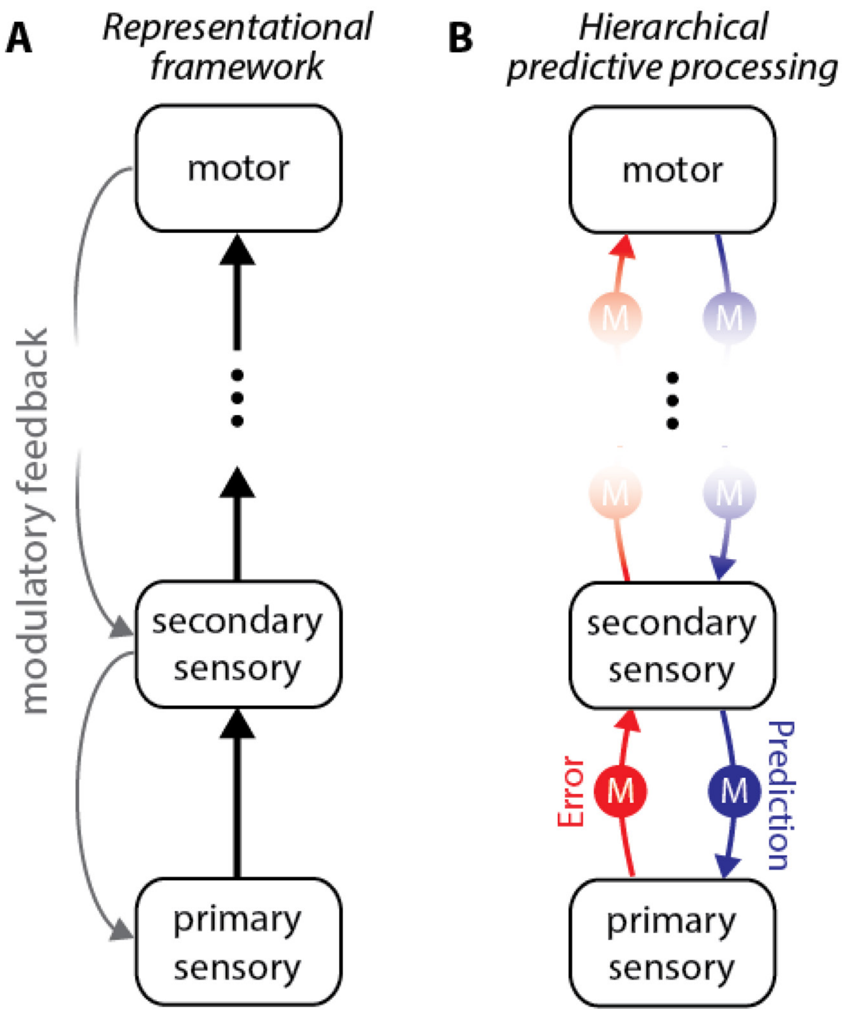


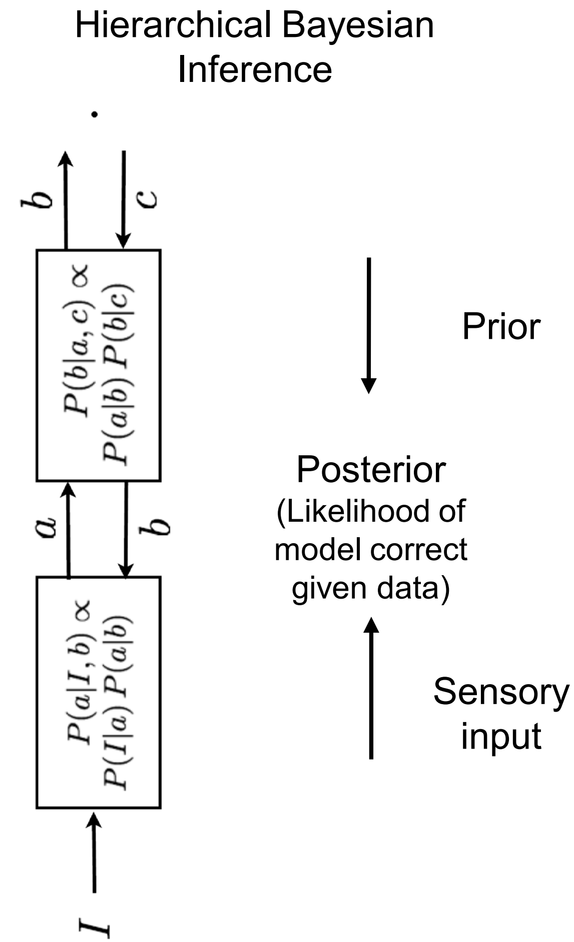
The importance of predictions for sensory perception

During eye or head movements:



Predictive Coding and Bayesian Inference

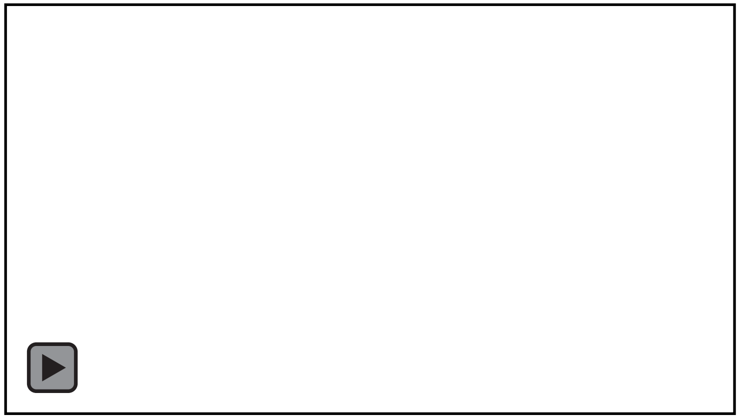


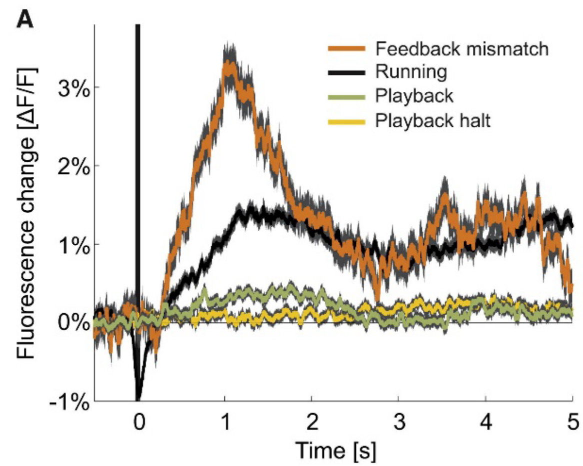


Kant, Helmholtz,…Friston, Clark, Mumford, Olshausen

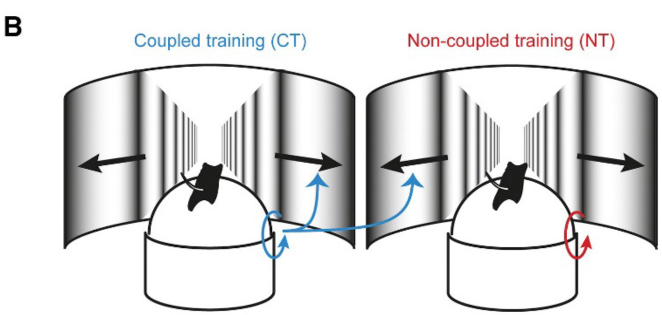
Predictive coding framework

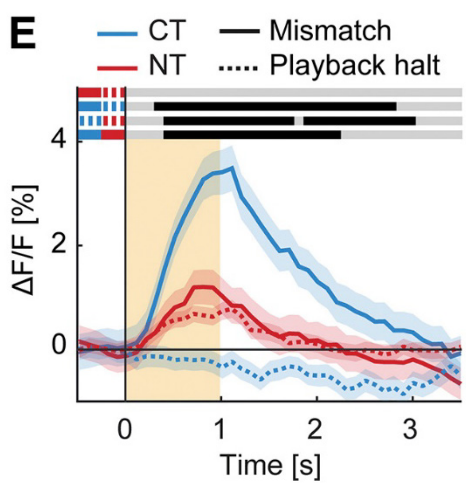
Experimental evidence for predictive coding in cortical circuits





A subset of neurons in V1 shows strong mismatch (prediction error) responses



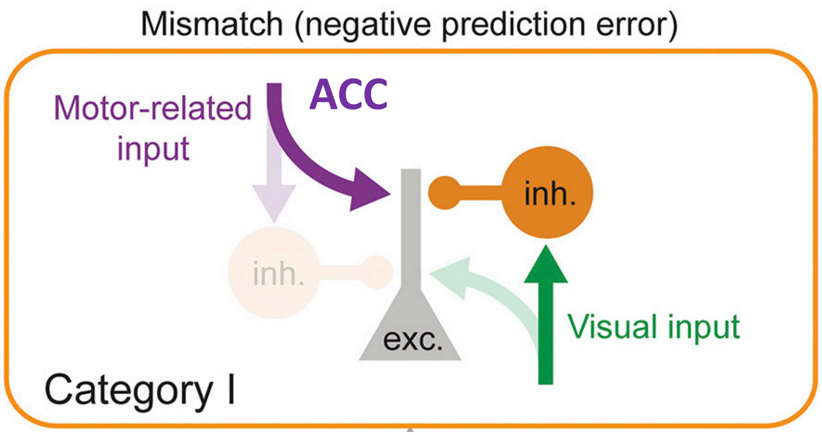


Mismatch responses are dependent on experience of visuo-motor coupling

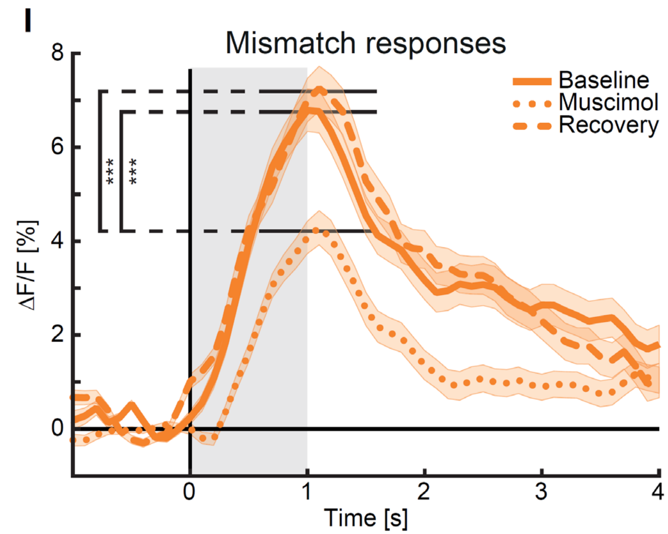
Keller et al., 2012
Attinger et al., 2017

Predictive coding framework

Potential circuit for mismatch computation in visual cortex



Muscimol in Anterior Cingulate Cortex (ACC)

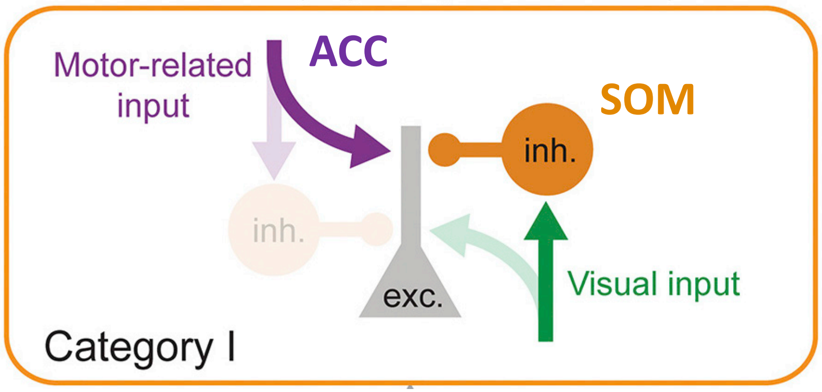


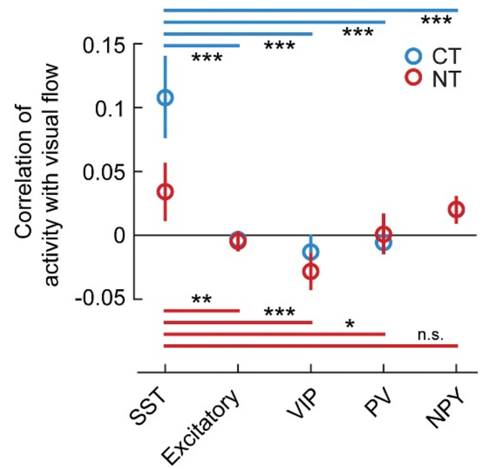
Mismatch response in V1 is weaker when ACC is silenced

Leinweber et al., 2017
Attinger et al., 2017

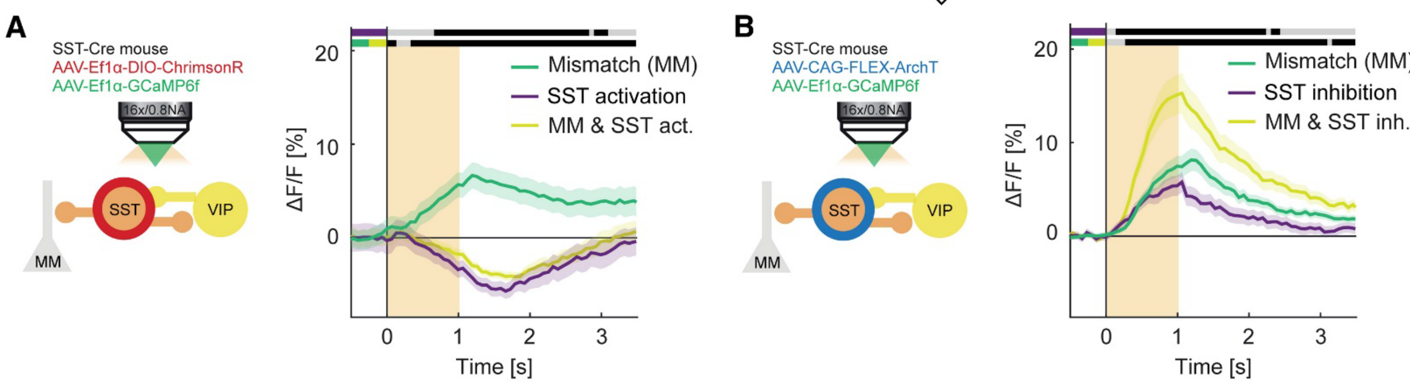
Predictive coding framework

Potential circuit for mismatch computation in visual cortex





Somatostatin (SOM) neurons are most strongly driven by visual flow



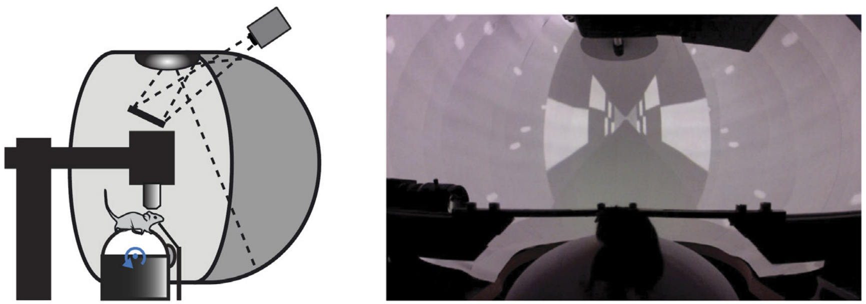
Optogenetic manipulation of SOM neurons alters mismatch response
(consistent with the model but no proof)

Attinger et al., 2017

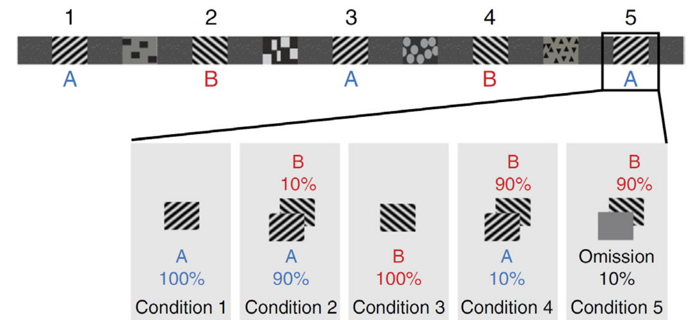
Predictive coding framework

Spatial prediction and prediction error signals in visual cortex

a

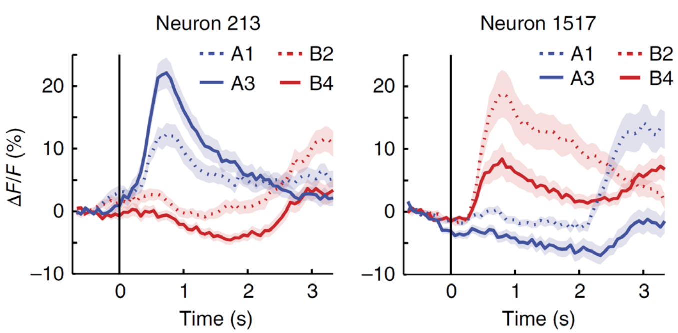


b



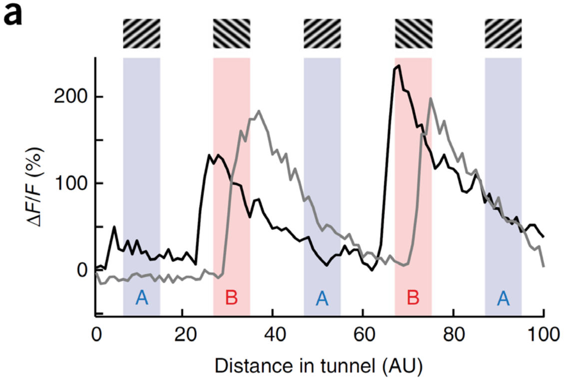
Some V1 neurons become selective to spatial location

d



Some V1 neurons start firing in expectation of visual stimuli

a



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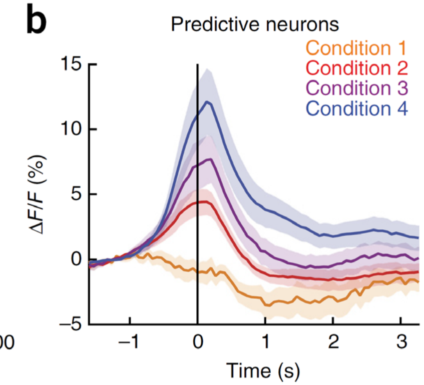
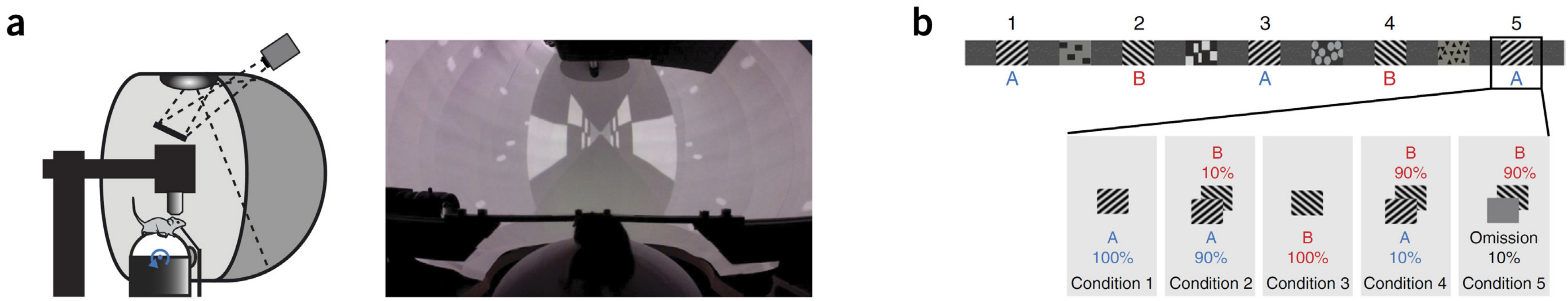


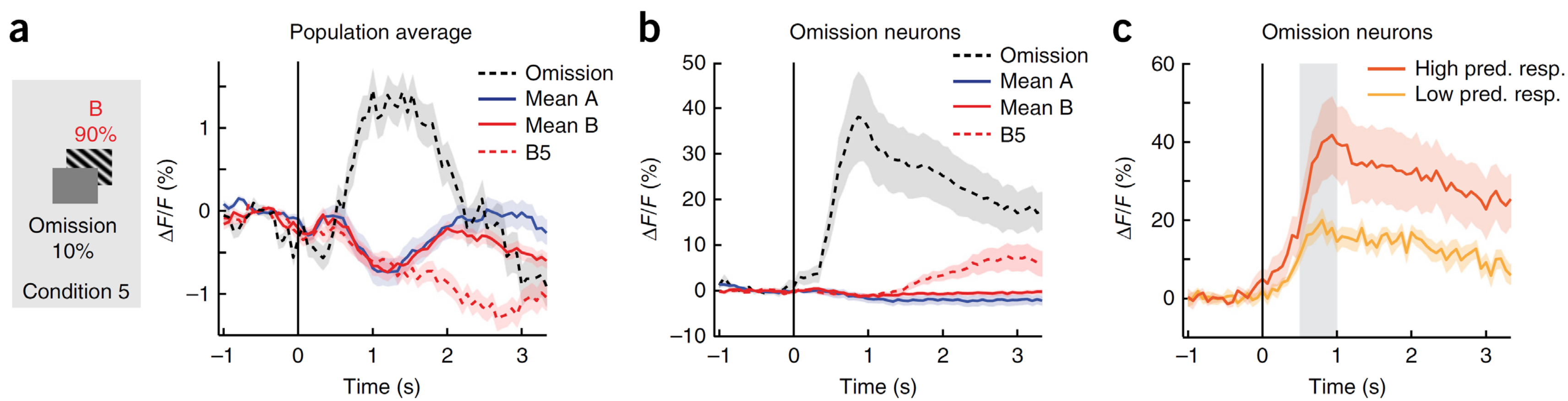
Fiser et al., 2016

Predictive coding framework

Spatial prediction and prediction error signals in visual cortex

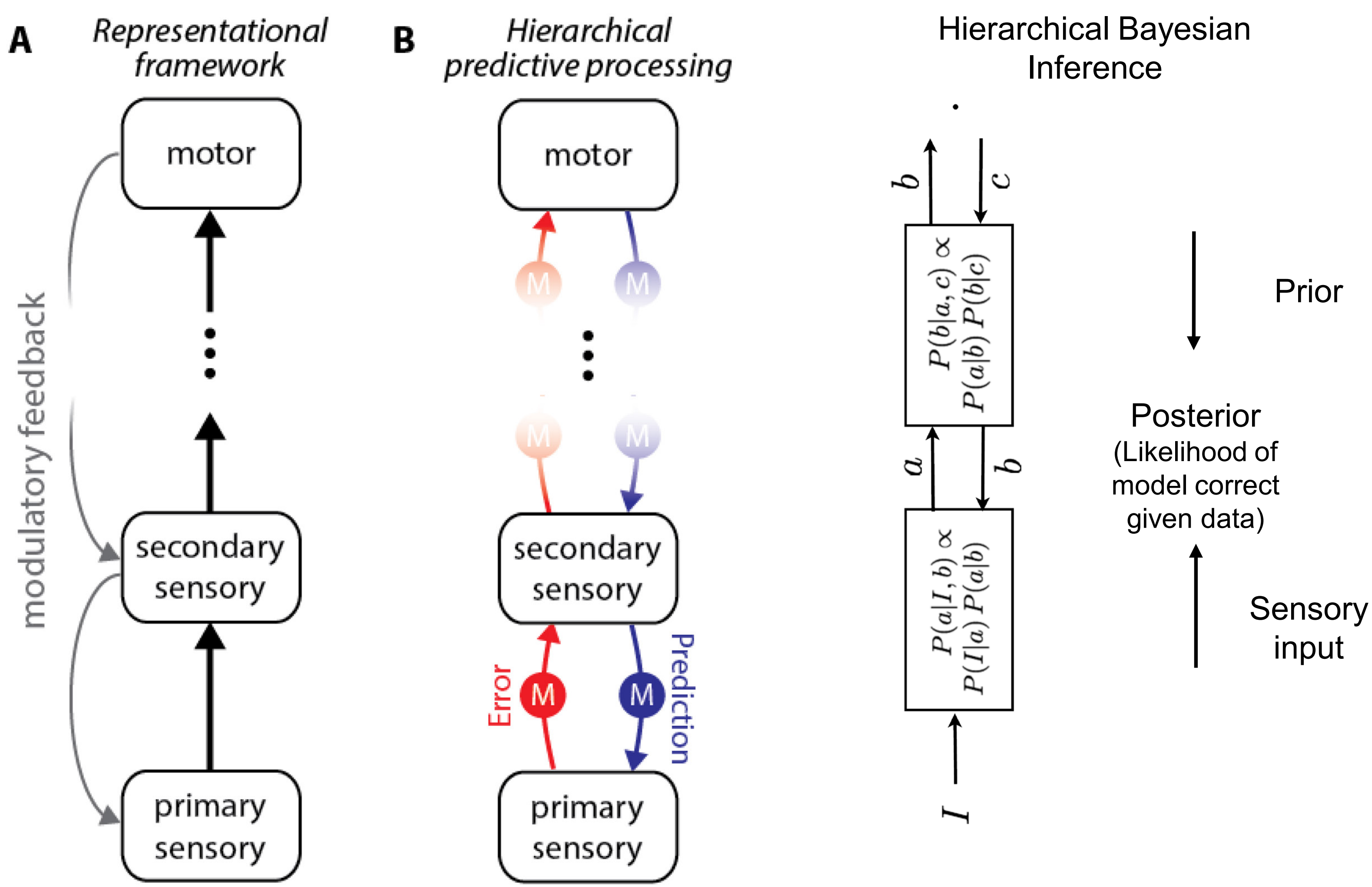


Strong response in V1 when an expected visual stimulus is omitted



Fiser et al., 2016

Predictive Coding and Bayesian Inference

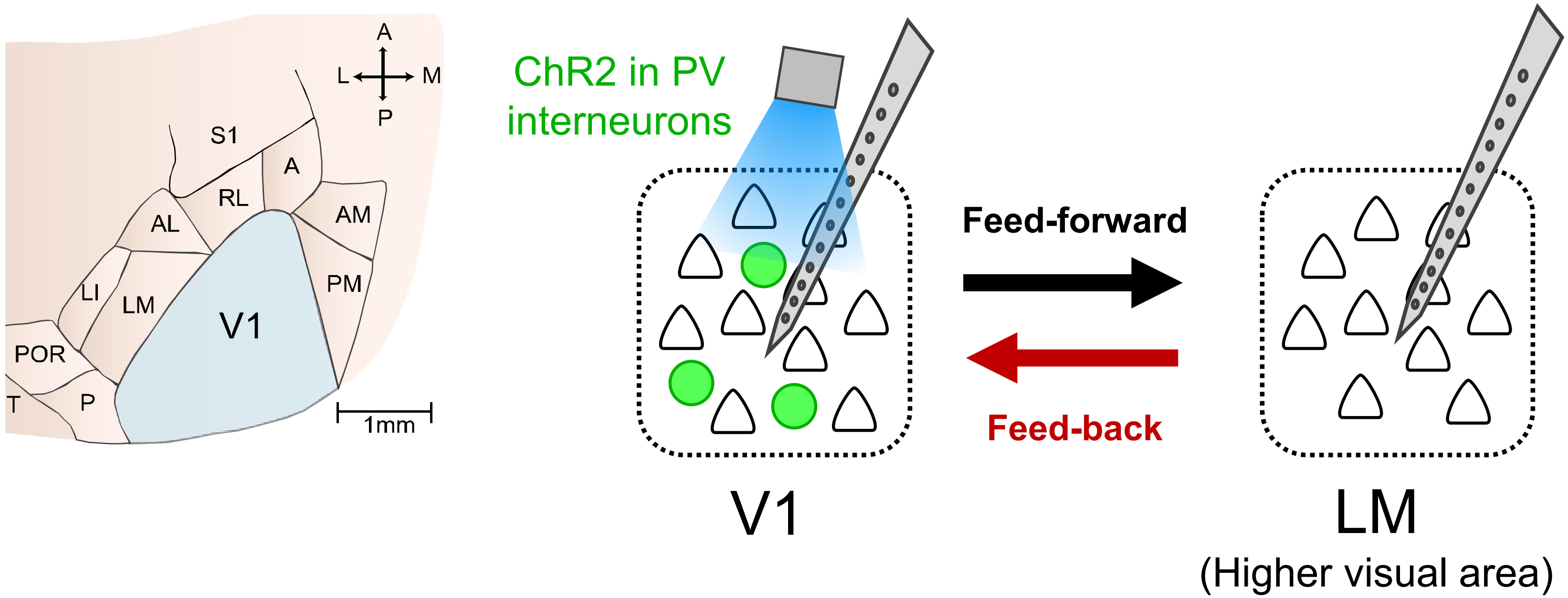


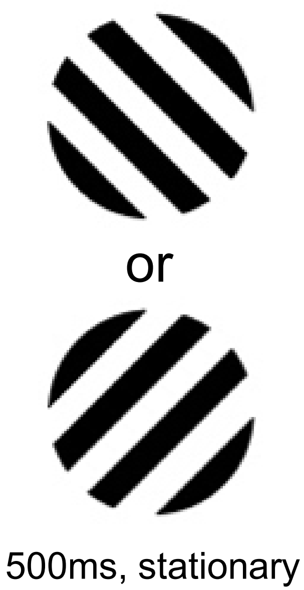
Kant, Helmholtz,…Friston, Clark, Mumford, Olshausen

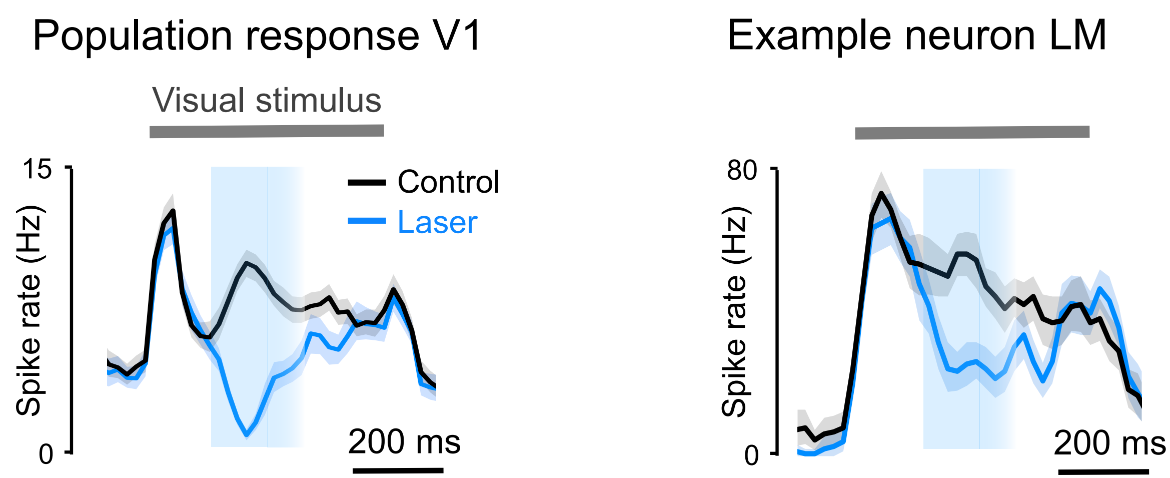
Feed-back projections

- What is the role of feed-back projections?
- How does feed-back influence the target area?
- How do cortical areas communicate? How dynamic is this communication? What is computed where?

A causal measure of effective inter-areal connectivity





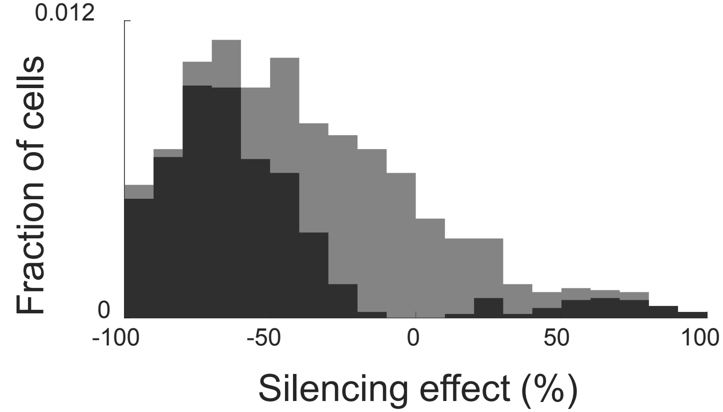


Influence of feed-forward vs feed-back projections

Feed-forward FF

V1 → LM

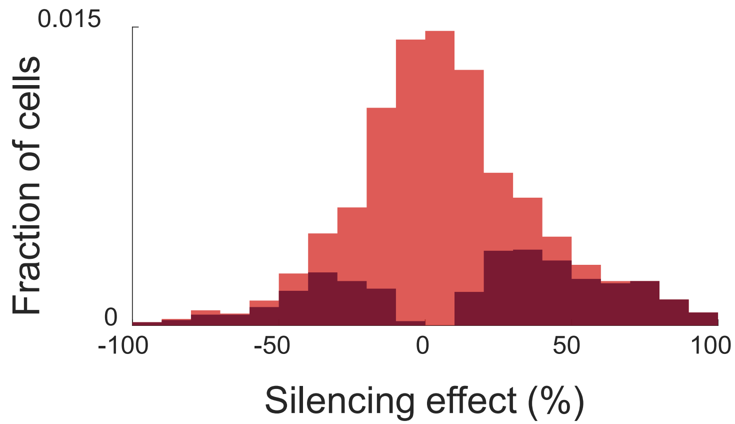
Silencing V1, Effect in LM



Feed-back FB

V1 ← LM

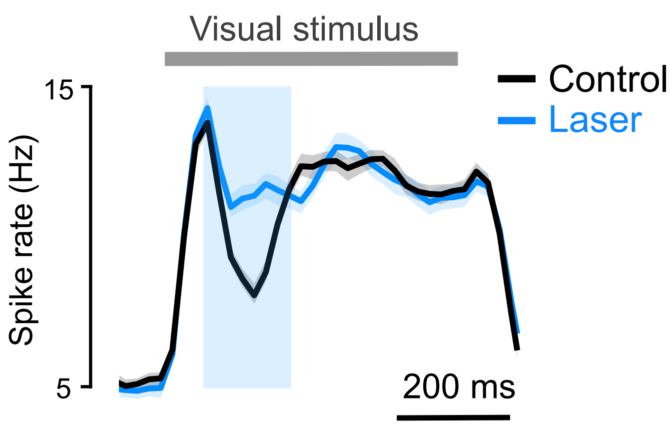
Silencing LM, Effect in V1



Feed-back suppresses responses and increases selectivity

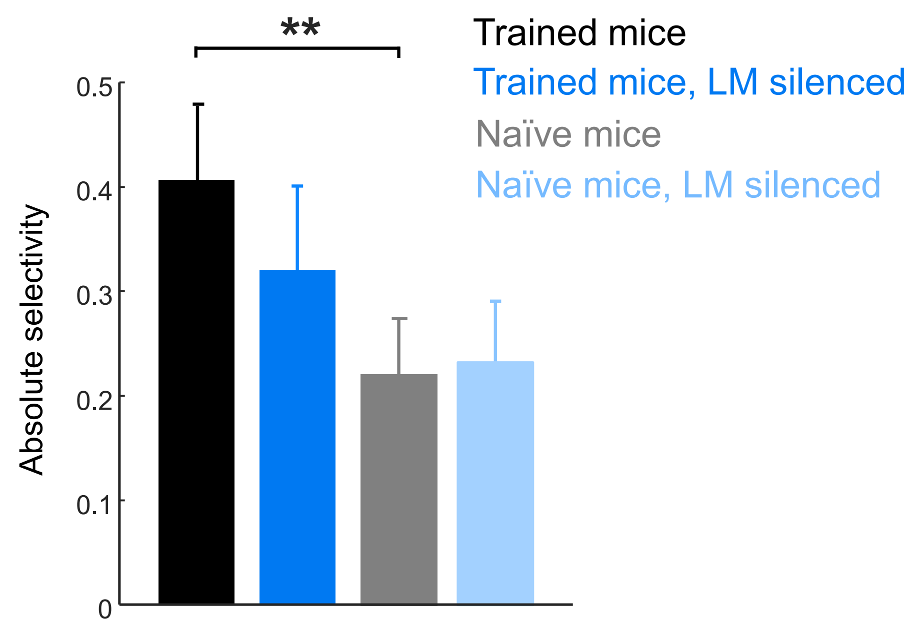
Average population response V1

Go stimulus, silencing at 60ms



Response selectivity in V1 Go - Nogo

(80-120 ms after stimulus onset)



- Feed-back influence is strongest when visual information is most relevant
- Feed-back increases selectivity in V1 after learning by suppressing responses, consistent with the predictive coding framework

Summary

- “Sensory” cortical areas are strongly influenced by context and behaviour
- Sensory processing is highly dynamic, allowing animals to flexibly access and process sensory information according to their current perceptual and behavioural demands.
- Still unclear to what degree top-down predictions influence or dominate sensory representations
- The sources of different internal signals are mostly still unknown and we are only starting to determine the circuit mechanisms of how some of these signals are integrated with sensory information
- Subcortical structures such as the superior colliculus, **thalamus**, cerebellum and the basal ganglia might also be important for shaping cortical information flow and integrating sensory and internal information

Further reading

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