V4A workshop

Error signals and adaption

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[1] r.gutzen@fz-juelich.de
INM-6, Forschungszentrum Jülich

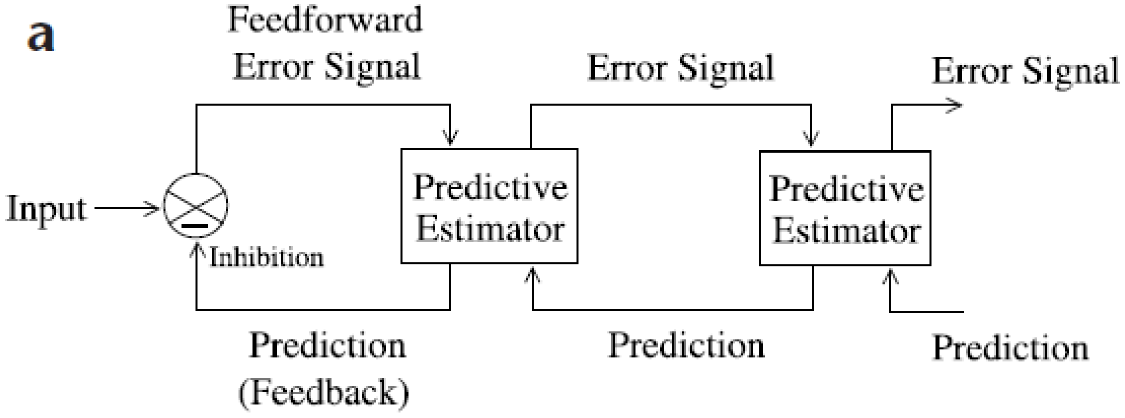
Prediction of and adaption to the ‘typical’ environment

- The brain can anticipate sensory input, i.e., formulate predictions of the immediate future
- General framework of how to think about brain $\rightarrow$ many flavors of hypotheses and approaches [see Clark, 2013]
- Early evidence of the predictive brain:
    - Spike frequency adaption to static input
    - Response suppression for repeated stimulus [Sokolov, 1960; [Miller, 1991]
    - Receptive field development to match natural environment [Switkes, 1978]
- Efficiency gain by not encoding a stimulus representation but only new information

Predictive Coding as hierarchical generative model [Rao & Ballard, 1999]

Basic model:

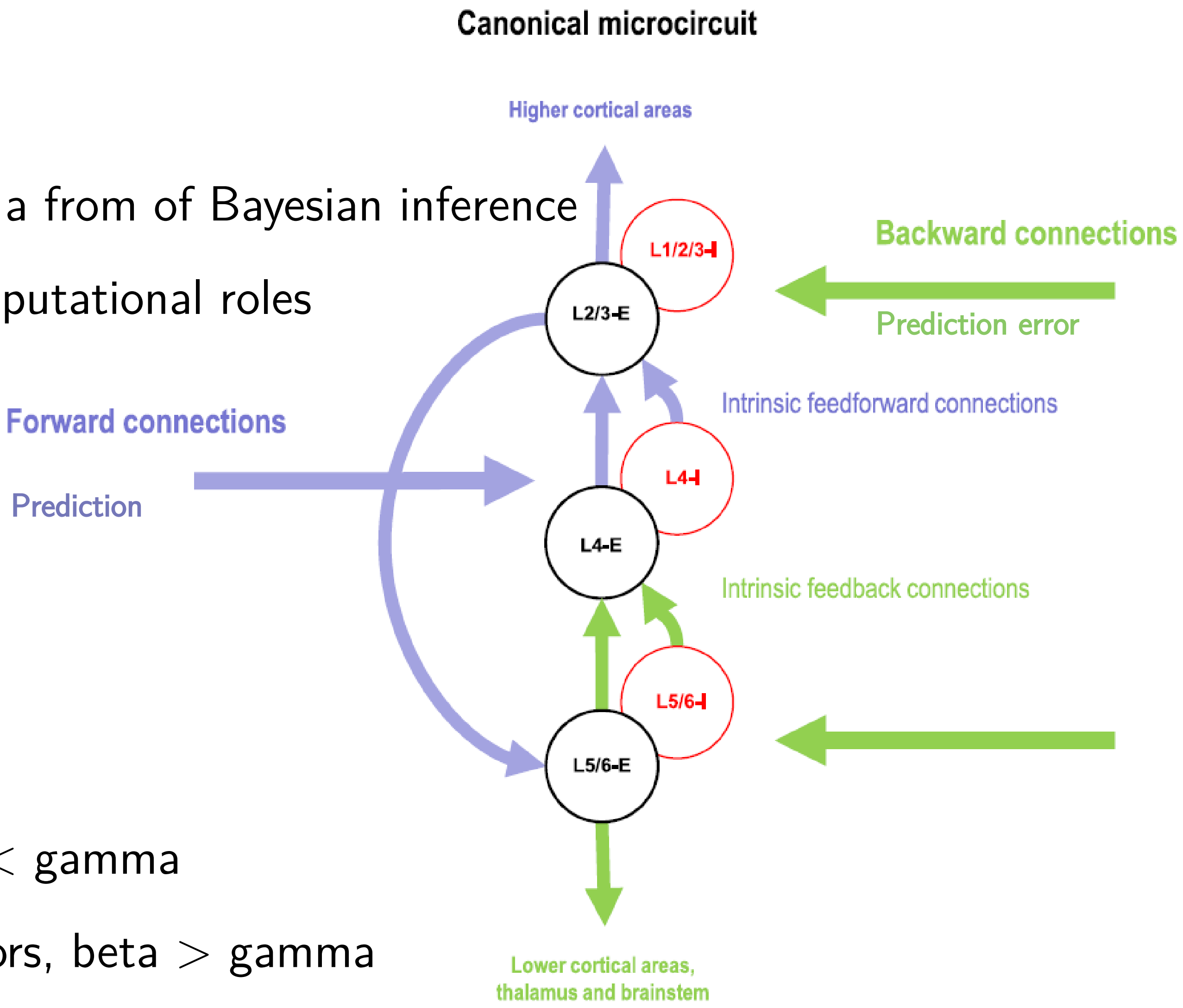
- Top-down feedback predicts activity in lower areas
- Feedforward signal carries prediction errors
- The internal model is continuously updated



Assumptions/postulations:

- Separate upstream and downstream pathways
- Existence of error-detecting neurons (likely in layer 2/3), distinct for positive and negative errors
- Prediction signals inhibit activity in lower areas, error signals excite higher areas

Predictive Coding in a canonical microcircuit [Bastos et al., 2012]



Idea:

- The cortical hierarchical organization implements a from of Bayesian inference
- Neuronal populations can be associated with computational roles
- The connectivity corresponds to the scheme of predictive coding

Assumptions/postulations:

- L2/3 encodes prediction errors
- L5/6 encodes predictions
- Feedforward: linear accumulation of errors, beta $<$ gamma
- Feedback: predictions $=$ non-linar function of errors, beta $>$ gamma
- Errors should express higher frequencies than the predictions that accumulate them

Evidence of error signals

Table 1. Electrophysiological and Neuroimaging Findings Consistent with Predictive Coding

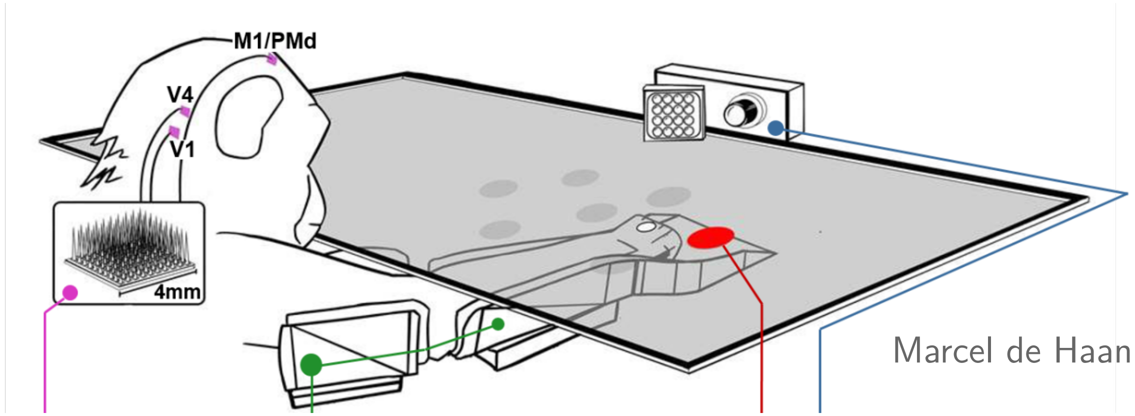
Prediction Violated	Area Studied	Neuronal Expression of Prediction Error	Study
Learned visual object pairings	Monkey inferotemporal cortex (IT)	Enhanced firing rate	Meyer and Olson, 2011
Natural image statistics	Monkey V1, V2, V3	Enhanced firing rate	Hupé et al., 1998; Bullier et al., 1996; Bair et al., 2003
Repetitive auditory stream	Early human auditory cortex	Enhanced event-related potentials (ERPs), enhanced gamma-band power	Garrido et al., 2007, 2009; Todorovic et al., 2011
Coherence of visual form and motion	Human V1, V2, V3, V4, V5/MT	Enhanced BOLD response	Murray et al., 2002, 2006; Harrison et al., 2007
Audio-visual congruence of speech	Visual and auditory cortex	Gamma-band oscillatory activity	Arnal et al., 2011
Predictability of visual stimuli as a function of attention	Human V1, V2, V3	Enhanced BOLD response when unattended, reduced BOLD when attended	Kok et al., 2012
Hierarchical expectations in auditory sequences	Human temporal cortex	Enhanced ERPs	Wacongne et al., 2011
Expected repetition (or alternation) of face stimuli	FFA in fMRI, parietal and central electrodes of EEG	Enhanced BOLD response, diminished repetition suppression of ERP	Summerfield et al., 2008, 2011
Apparent motion of visual stimulus	V1	Enhanced BOLD response	Alink et al., 2010

Bastos et al., 2012

- Prediction violation $\sim$ ‘more’ activity
- How about synchrony, spiking patterns, phase locking, inter-area communication, ... ?

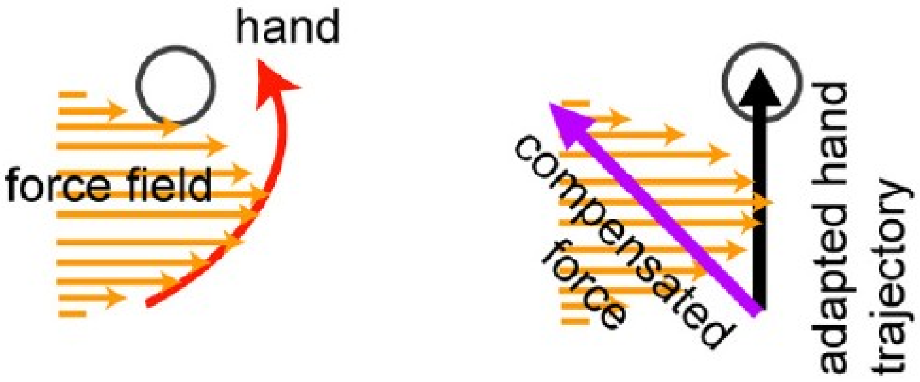
Investigating error signals in the V4A experiment

- Behavioral
  - Movement trajectory adaption to perturbation?
  - Influence of visual feedback?
  - Compensation to force introduction vs. removal?
  - Comparison to behavioral model?
- Cortical
  - Activity change while/after perturbation?
  - Activity change in preparation of adaptive movement exec.?
  - Correspondence of the activity changes to specific movement?
  - Decrease of activity changes during relearning?
  - Comparison to neural network model?



Marcel de Haan

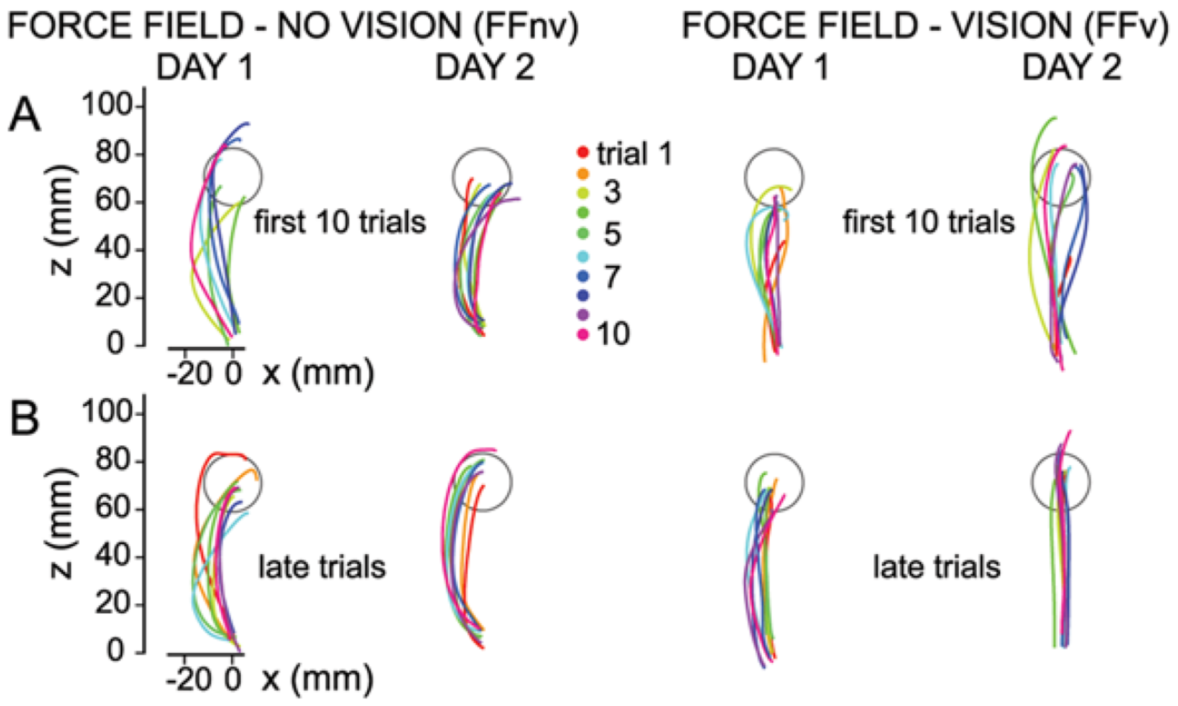
With and without visual feedback



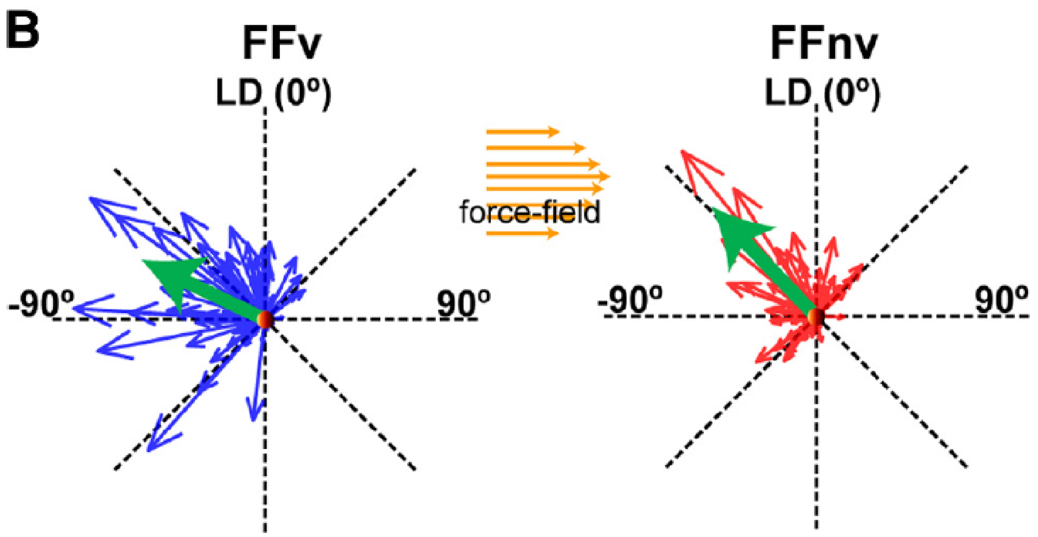
Arce et al., 2010

Reference studies Arce et al. 2009, 2010

- Experiment:
  - Pointing task with humans and macaques (Eph. in M1)
  - Force-field perturbation
  - With (v) and without (nv) visual feedback



- Results:
  - Adaptive trajectories remain curved without visual feedback
  - Tuning curves of neurons are unchanged
  - Population vector is reorganized to compensate force-field
  - (v): more force compensation and on-the-fly corrections
  - (nv): more focus to adaption of final hand position



Other reference studies for perturbed arm movement

- Orban de Xivry et al. 2011

  Effect of disruption (TMS) on M1 during rapid/gradual perturbation adaption in a pointing tasks (human)
- Torrecillos et al., 2015

  Influence of different induced errors in a shooting/pointing task on beta activity (human, EEG)
- Tseng et al, 2007

  Sensory vs. motor errors in shooting/pointing task with visiomotor rotation (human w/wo cerebellar ataxia)
- Schlerf et al., 2012

  Increased activity in cerebellum for both unexpected presence or absence of force pulse (human, fMRI)

Some of the points to discuss...

- What are the most intriguing/ most tractable questions to investigate?
- What is the likelihood to finding evidence in support or against a corresponding hypothesis?
  - Are there valuable low-risk contributions along the way? (re-learning, influence of visual feedback, comparisons to models, signs for alternative corrective instructions, ...)
- What can be realized with the kin-arm setup?
  - What force to apply? (force-field shape, strength)
  - How to apply and remove the force? (single random, continuous, gradual)
- Compatibility to monkey training
  - Expected response of monkey? (frustration, reduced learning, ...)
  - At what stage could perturbation be introduced?
  - Availability of 2nd monkey?
- Potential models to apply

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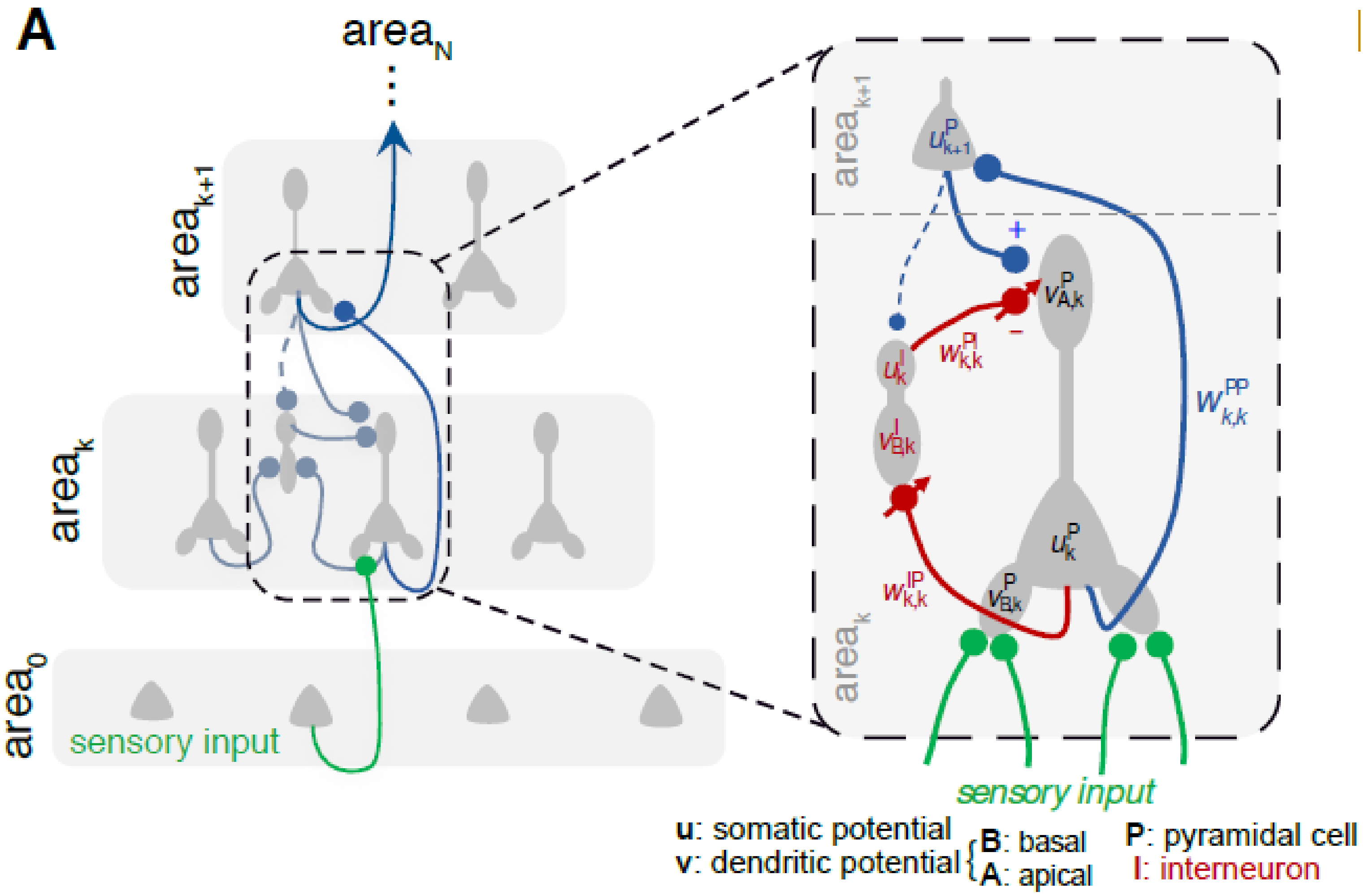
Predictive Coding via dendritic integration and lateral cancellation

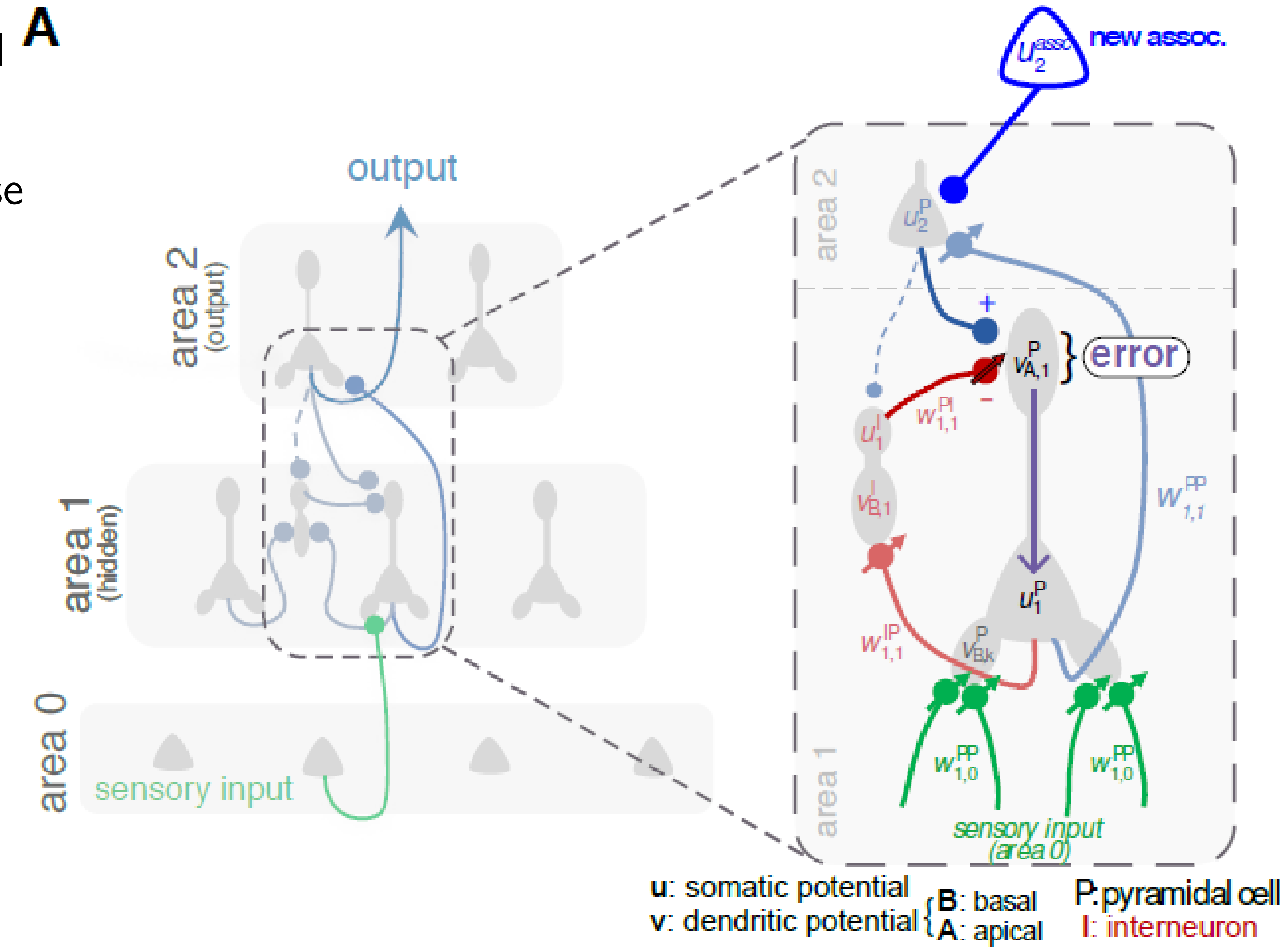
Inter-neurons which mimic higher area activity can cancel top-down feedback in a self-predicting network, independent of the input



Sacramento et al., 2018

Predictive Coding via dendritic integration and lateral cancellation

Additional top-down signals can't be canceled and cause dendritic errors, which are propagated to lower areas and cause synaptic learning.



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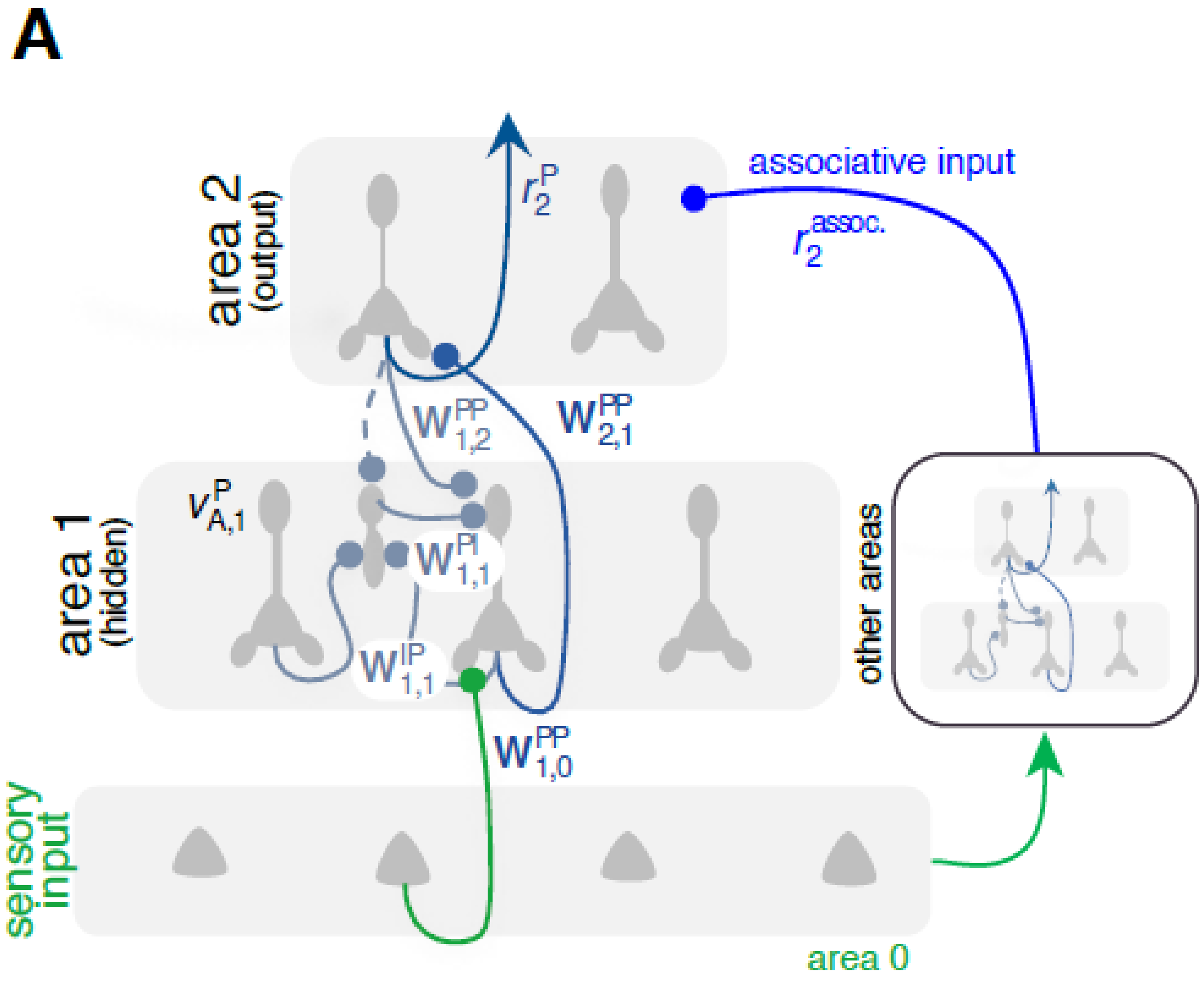
Predictive Coding via dendritic integration and lateral cancellation

Such top-down signals can be understood as the output of other areas transforming the same sensory input.

Assumptions/postulations:

- Lateral interneurons cancel top-down signals
- Disassociation between areas would cause adaptions of interneuron connections
- Cancellation signals need to have the exact same magnitude and delay as top-down signals



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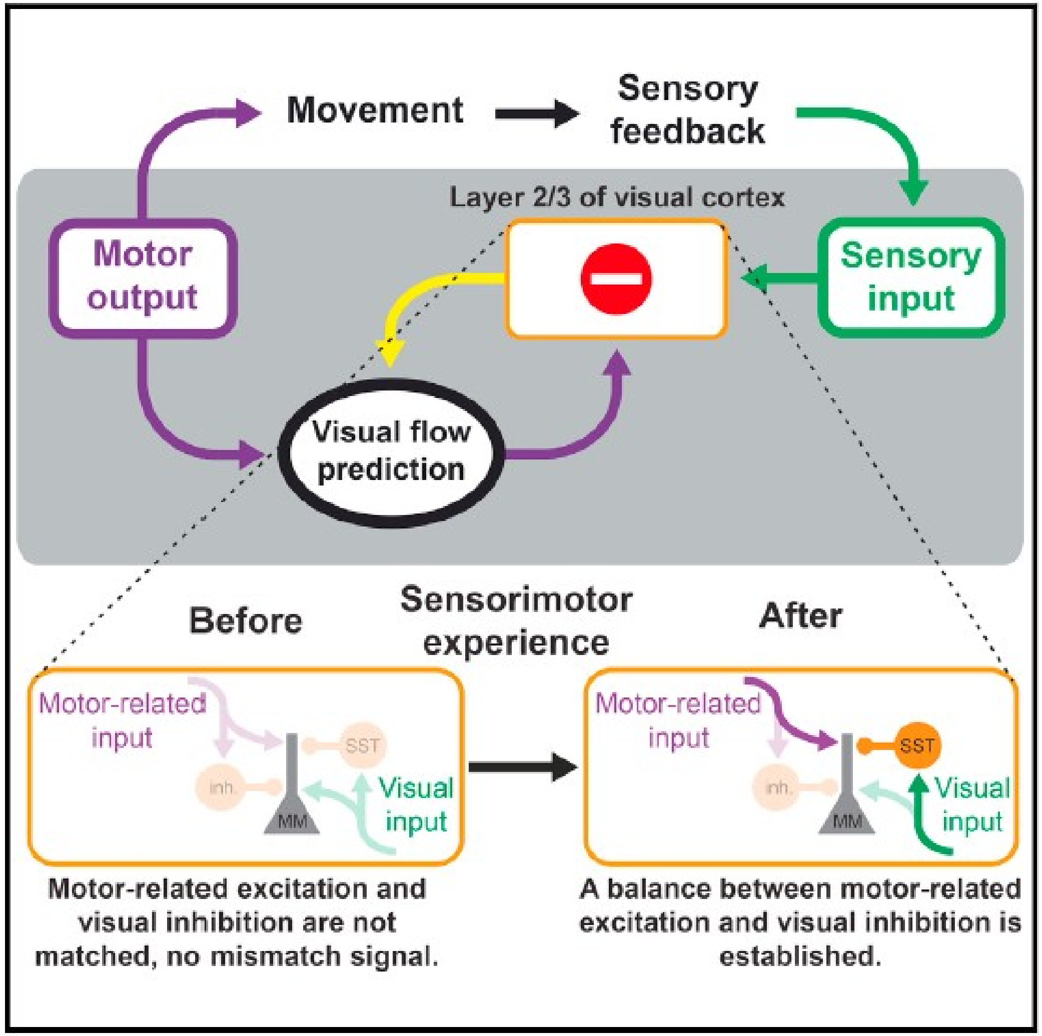
Visuomotor Coupling Shapes the Functional Development of Mouse Visual Cortex

Graphical Abstract



Authors

Alexander Attinger, Bo Wang, Georg B. Keller

Correspondence

georg.keller@fmi.ch

In Brief

The coupling of sensory and motor experience during development shapes visual perception by tuning a cortical circuit that compares inhibitory visual input and excitatory motor input and is able to detect mismatches between actual and expected sensory experience.

Example experiment design

- Task: Move hand to target. Targets are activated randomly, but with a fixed rhythm irrespective of successful reaching
- Perturbation: Uniform force-field from the right side (left as control)
- Introduce perturbation at random point in time, and keep it at least as long as the behavior is fully adapted
- Remove perturbation and not reintroduce it until the behavior adapted again
- In other sessions, make the glass plane non-transparent so that the monkey doesn't have visual feedback about the arm's location

Example analysis plan

- First look for general activity modulation
  - Expect error signals in perturbation trials after/while movement execution (excitatory, upstream, in superficial pyramidal cells, layer 2/3, high frequencies)
  - Expect prediction/correction signals after initial perturbation trials in preparatory period (inhibitory, downstream, in deep pyramidal cells, layer 5/6, low frequencies)
- Test if these specific activities decrease in the same manner as the movement trajectory is adapted to the perturbation
- Search for cancellation signals (inhibitory lateral mirror-signals of top-down signals)
- ...