A Theory of How Active Behavior Affects Neural Dynamics:

Neural Gain Modulation by Closed-loop Sensory Feedback

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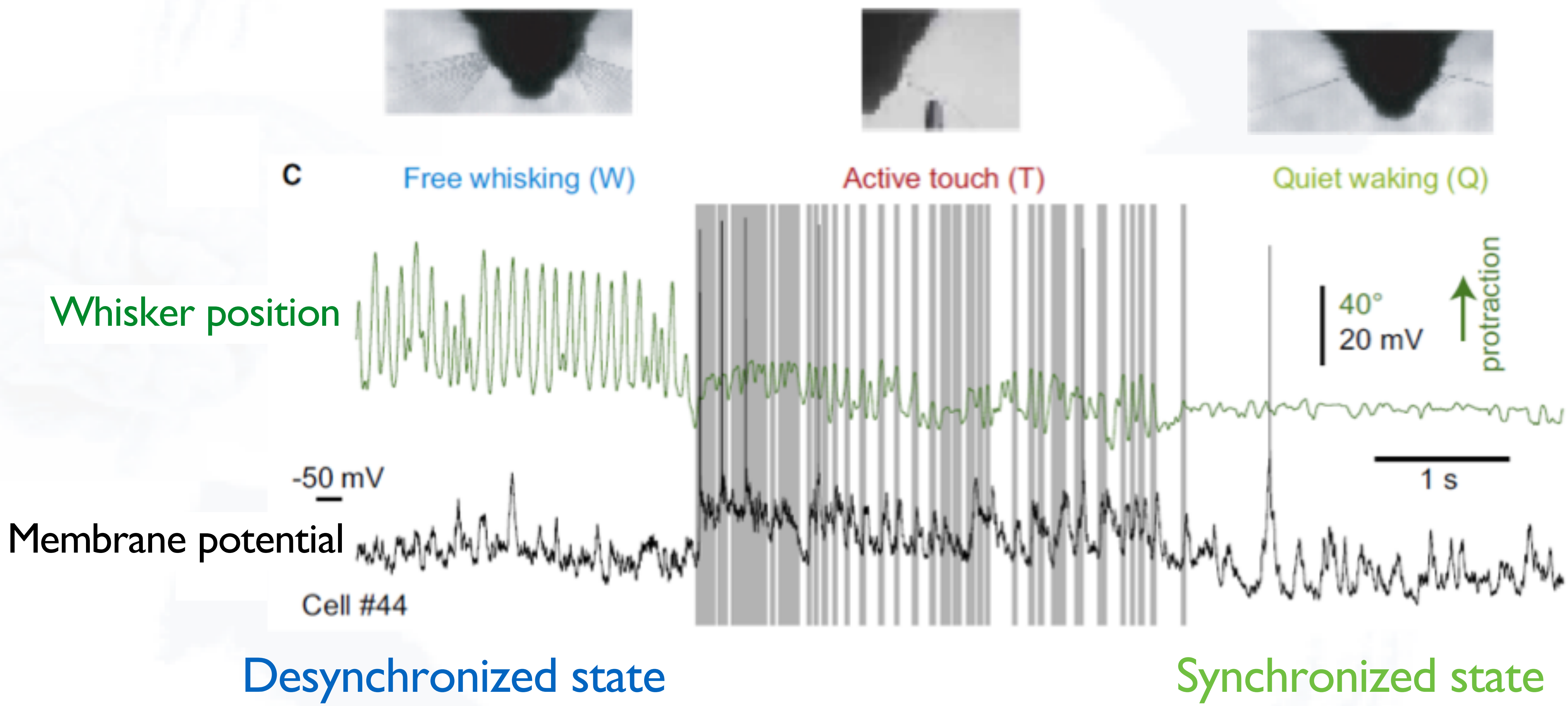
Animals behave passively or actively in the environment.

Neural dynamics are different during active and passive behaviors.

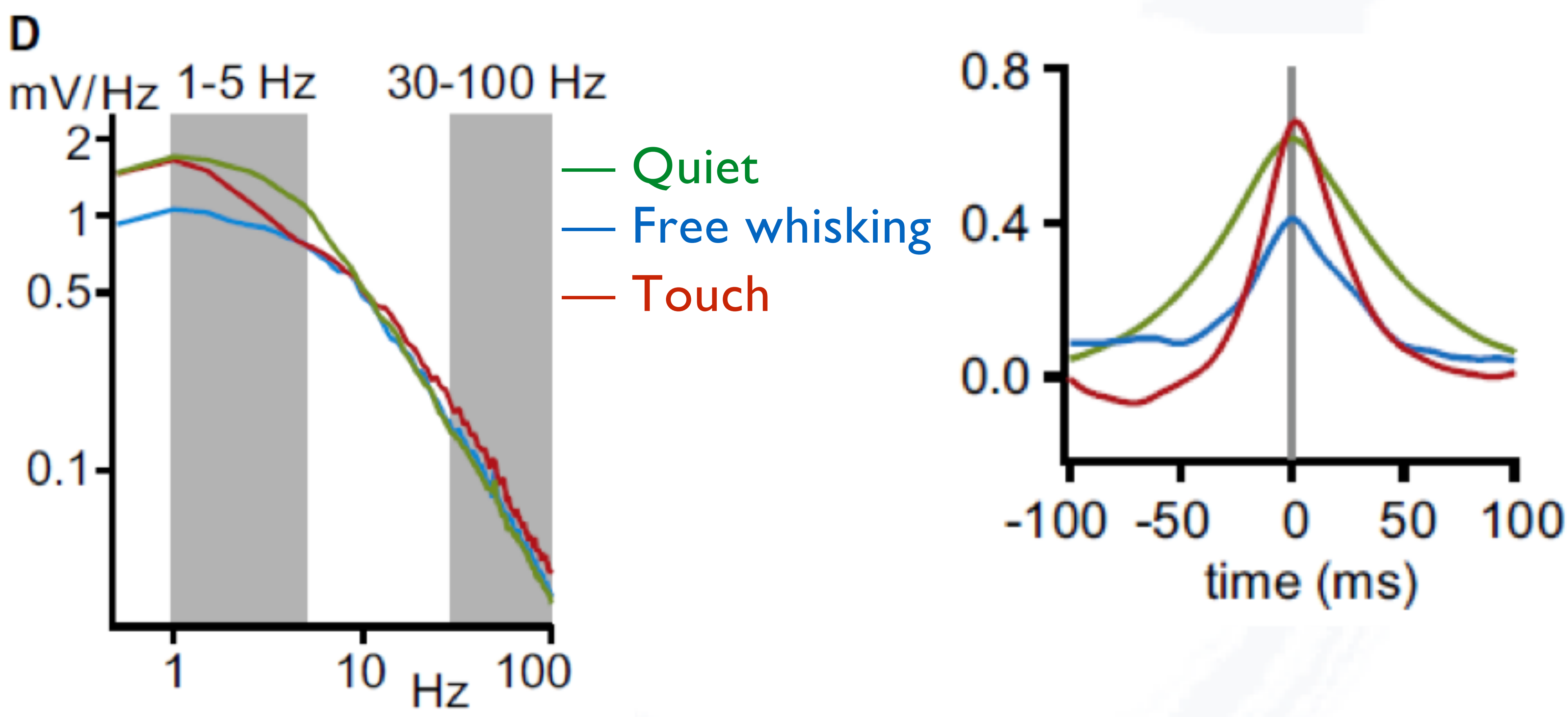
Whisking triggers a brain state transition.



Poulet and Petersen 2008; Crochet et. al. 2008, 2011

(1) Whisking suppresses coherent neural fluctuations.

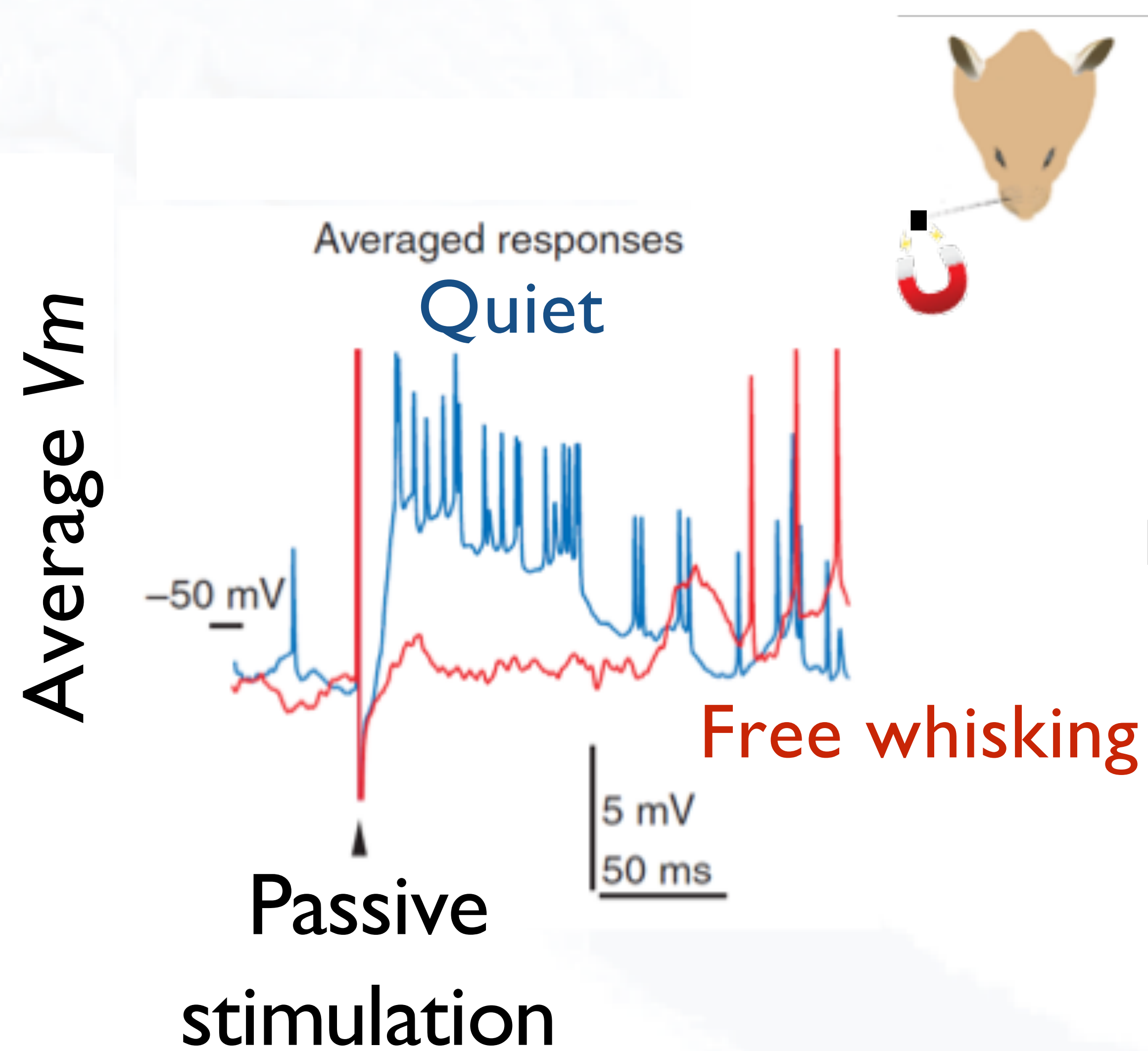
***Vm* power spectrum** — **pairwise *Vm* correlations**



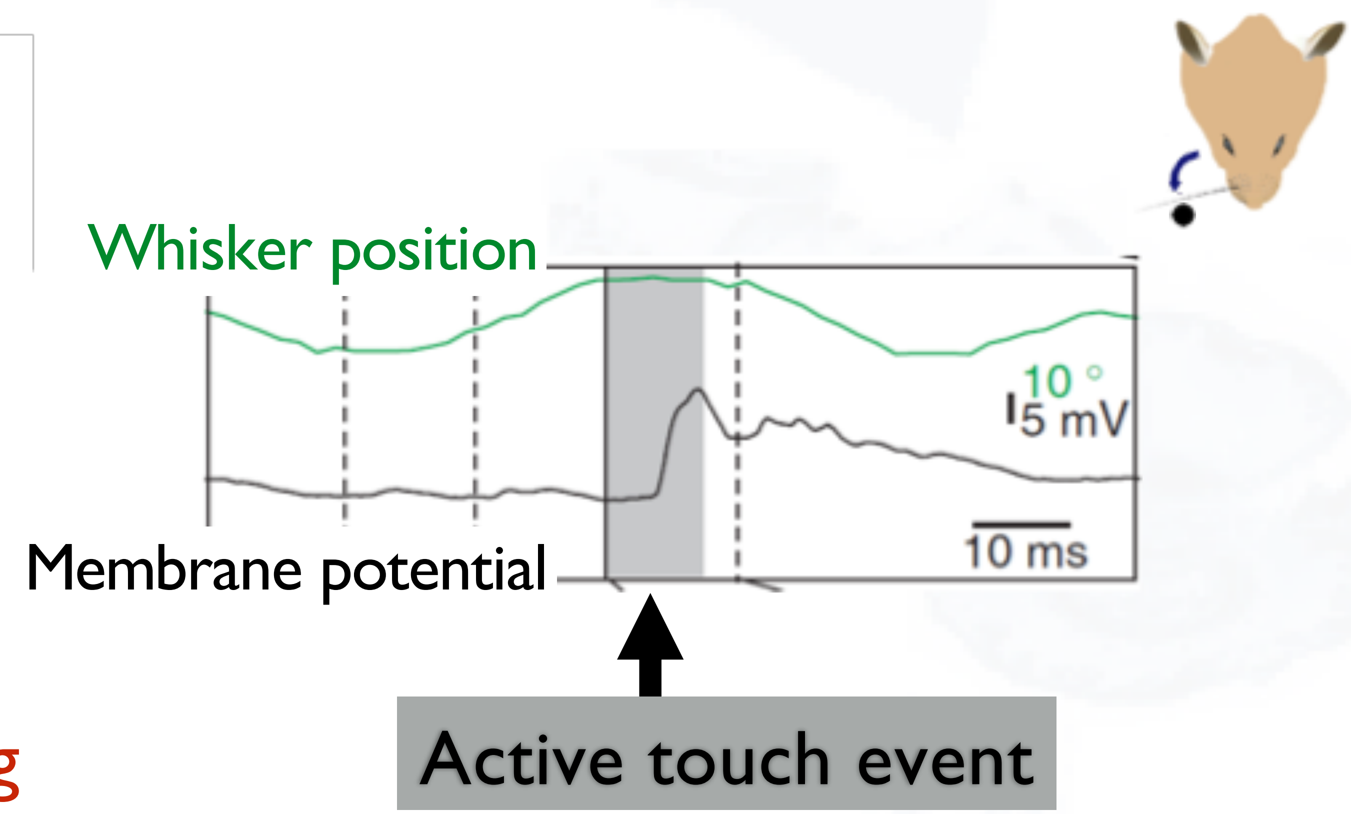
Poulet and Petersen 2008; Crochet et. al. 2008, 2011

(2) Whisking suppresses sensory response to passive whisker stimulation. However, an active touch is accentuated.

Passive whisker deflection

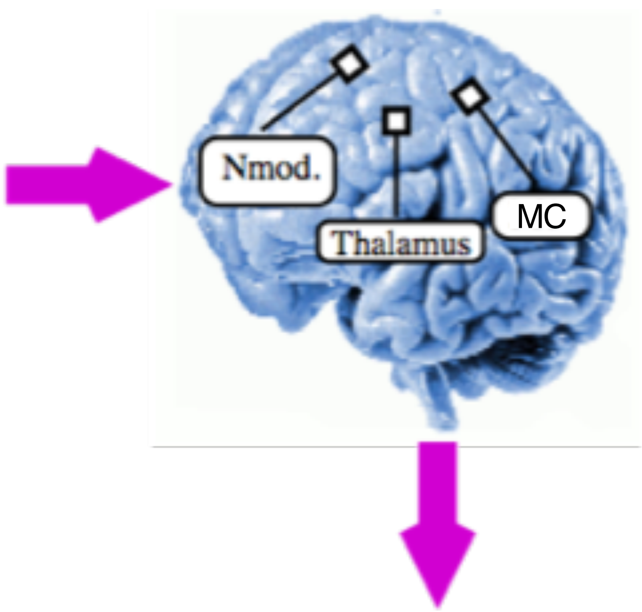


Active touch



Crochet et. al. 2006

Multiple mechanisms for a brain state transition



○ Internal:

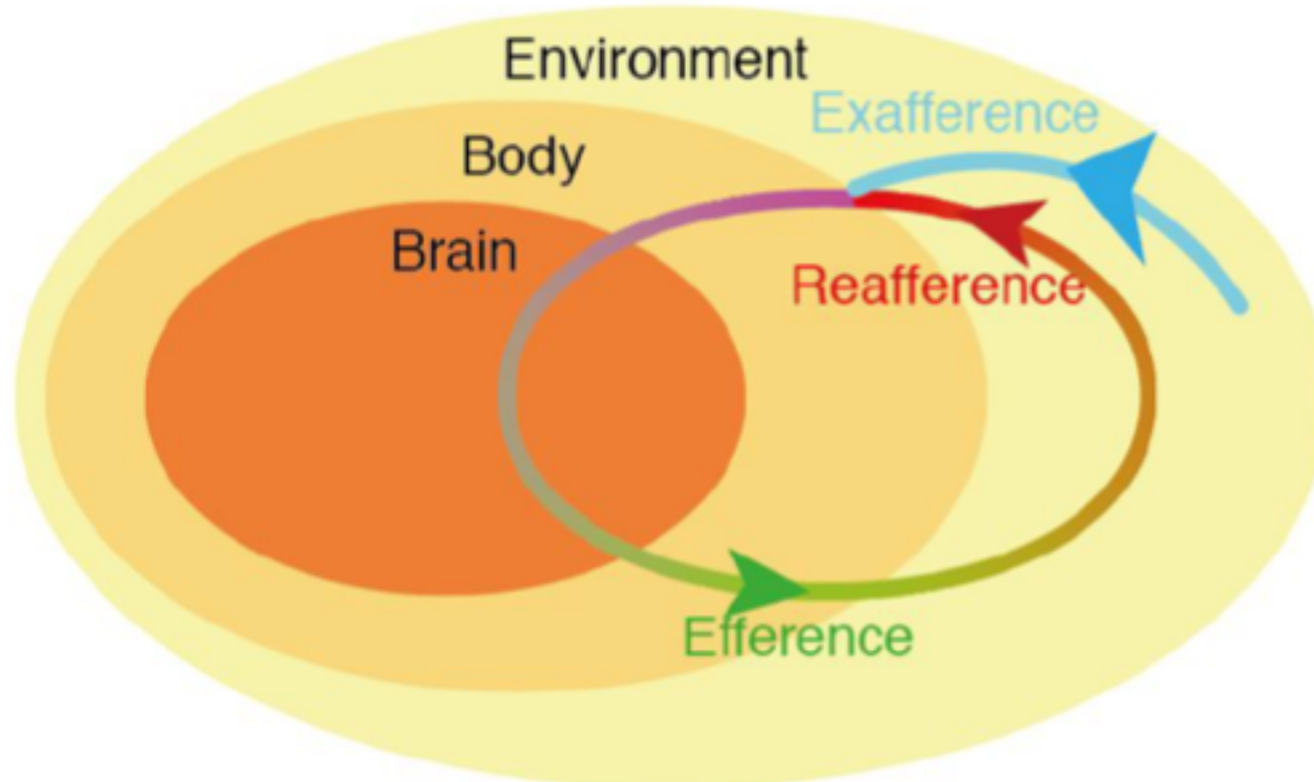
- Neuromodulators (Pinto et. al, 2013; Fu et al. 2014)
- Thalamocortical input (Poulet et. al. 2012)
- Intracortical feedback from motor cortices (Zagha et. al. 2013; Schneider et al. 2014)

○ External:

- Sensory input (Churchland et al. 2010, Tan et al. 2014)

No single mechanism is likely necessary.
Here we investigate the problem from a dynamical systems view.

Closed-loop sensory feedback

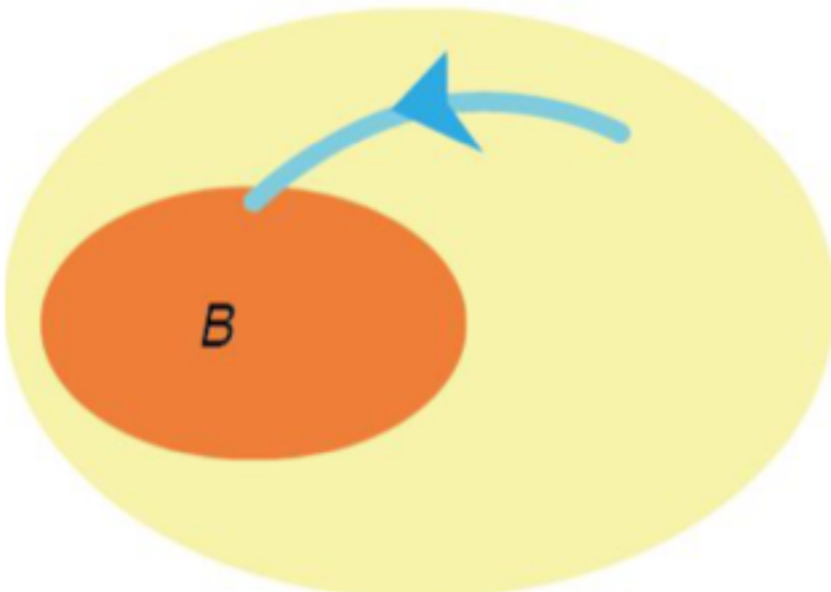


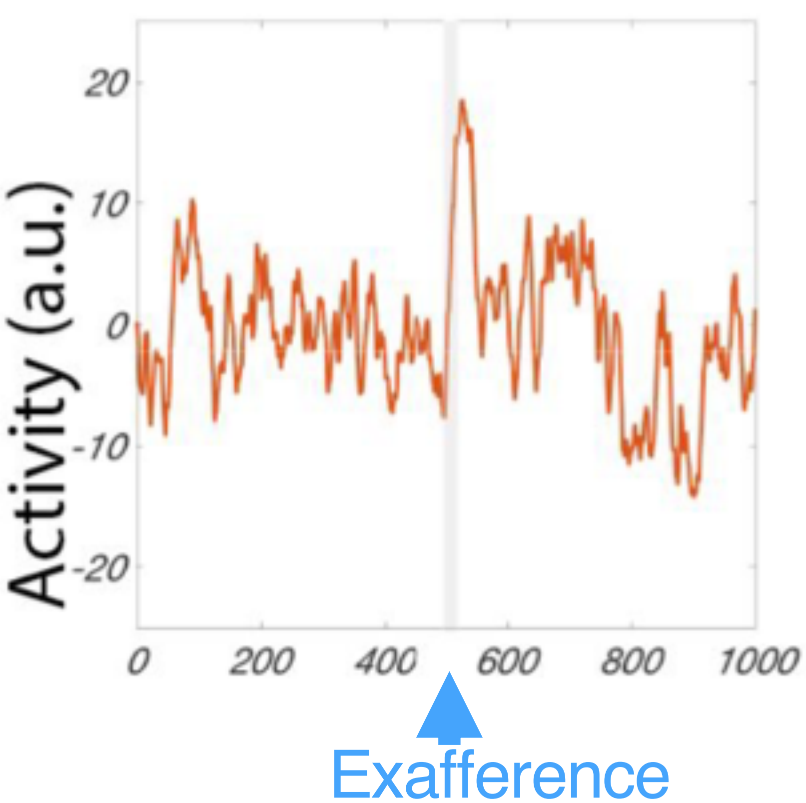
Sensory feedback of animal's action is strongly represented in the thalamus and cortex.
(Kleinfeld et. al. 2006; Gutinsky et al., 2013; Peron et al. 2015)

We hypothesize that the closed-loop sensory feedback mediated by the body/environment plays a role in the brain state transition.
(Buckley and Toyoizumi 2018)

Theory:
Negative sensory feedback reduces neural gain.

Open loop



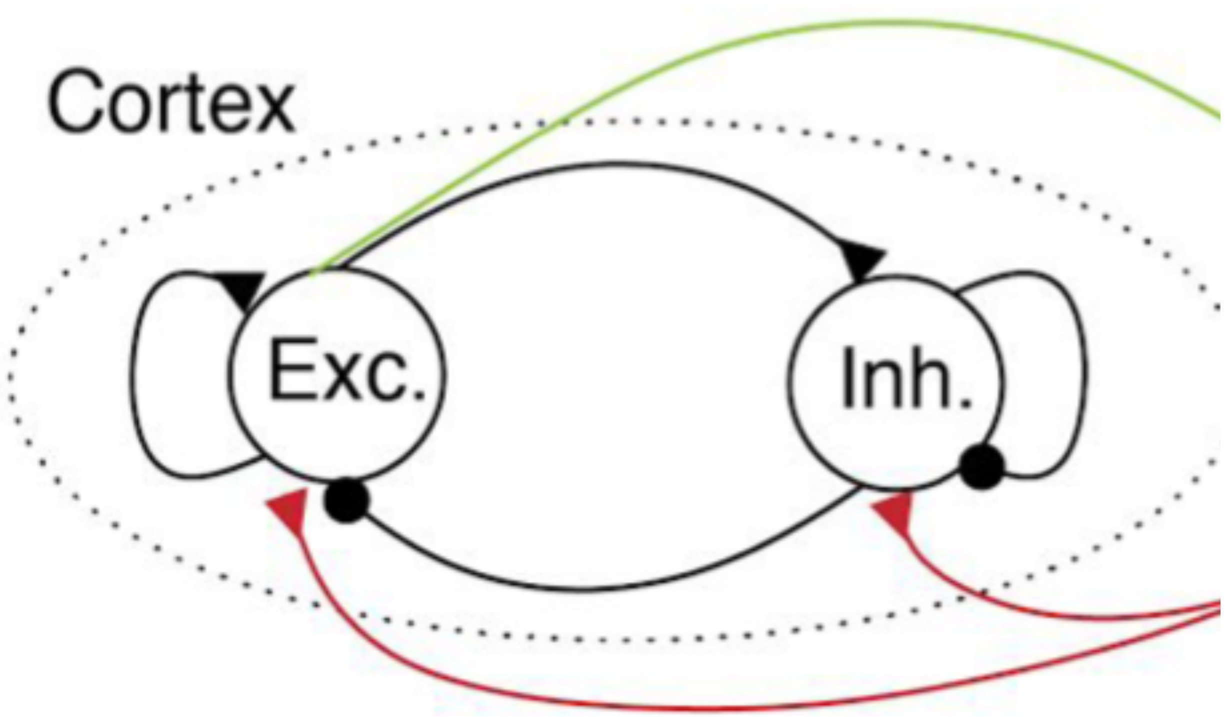


time (a.u.)

A simple model of the whisker system

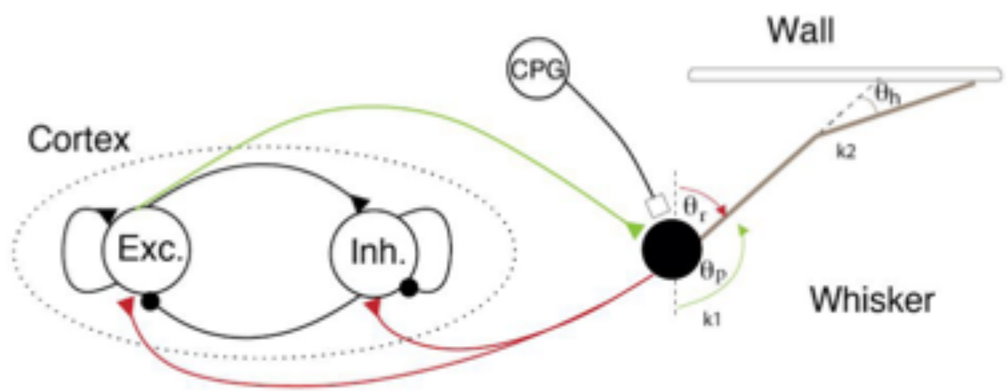
CPC

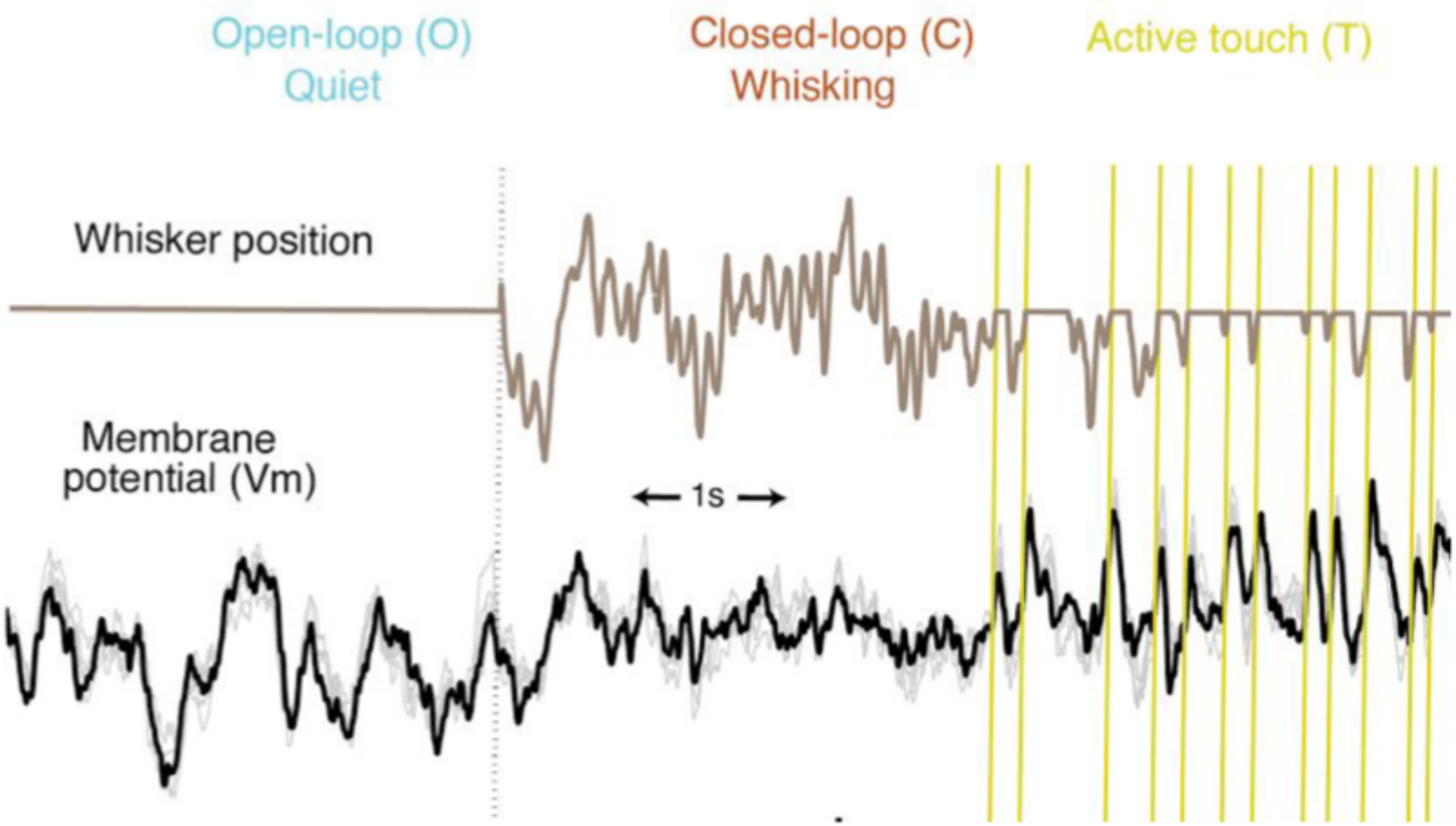
Neurons exhibit slow (~1s) adaptation.



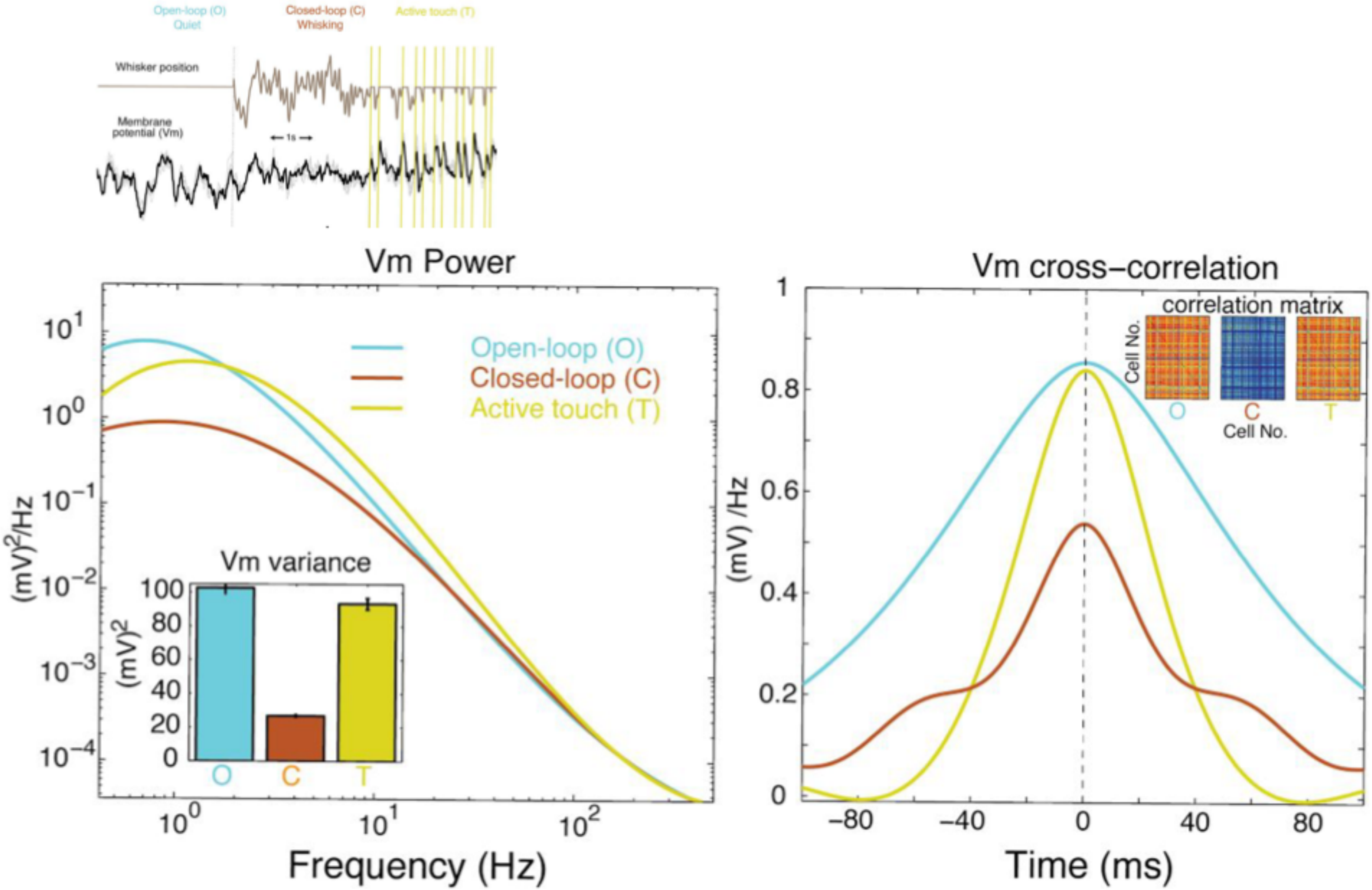
We assume that negative sensory feedb
is mediated by whisking vibrissa.

The model reproduces the membrane potential dynamics.





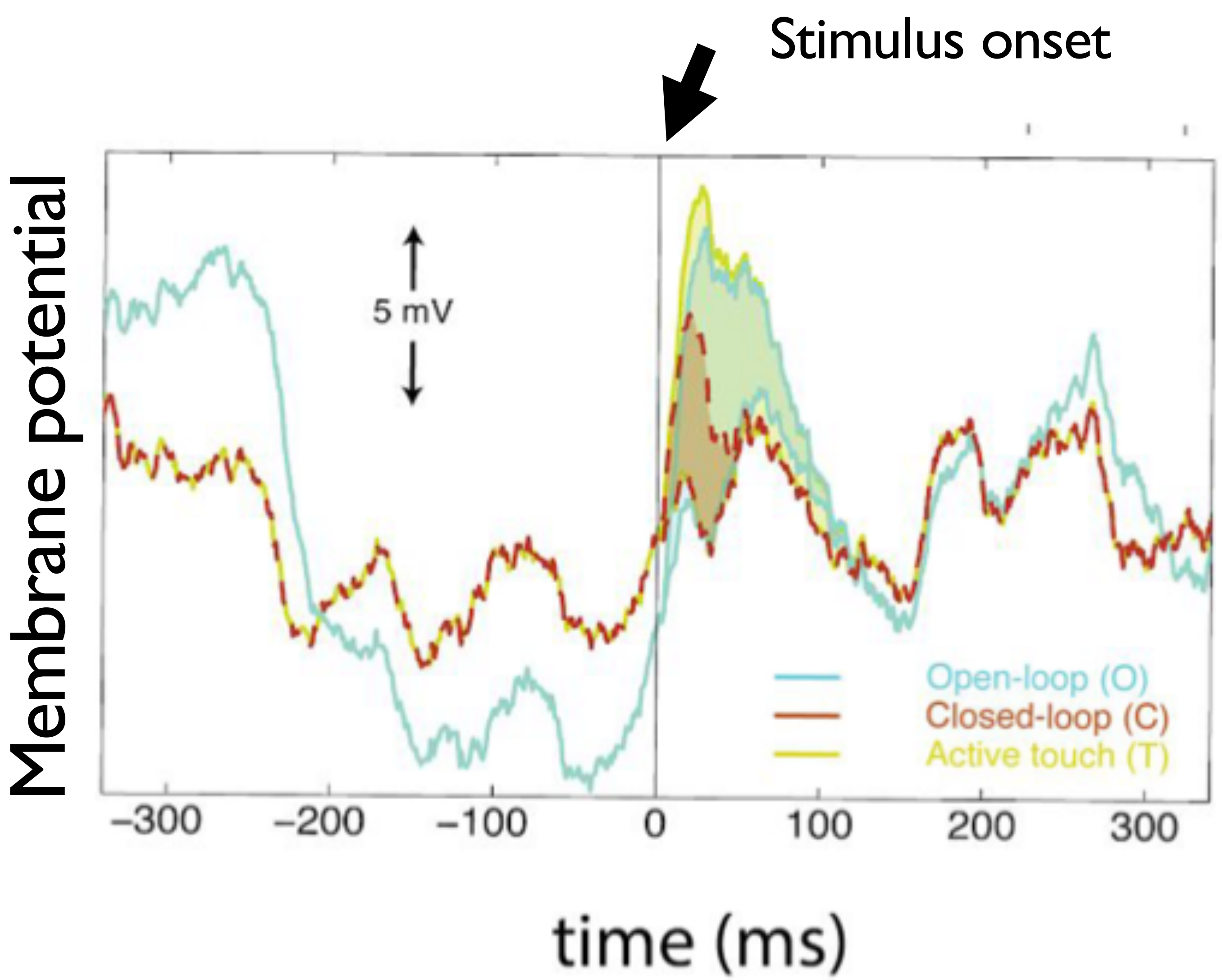
Closed-loop sensory feedback can suppress coherent neural fluctuations.



(Buckley and Toyoizumi 2018)

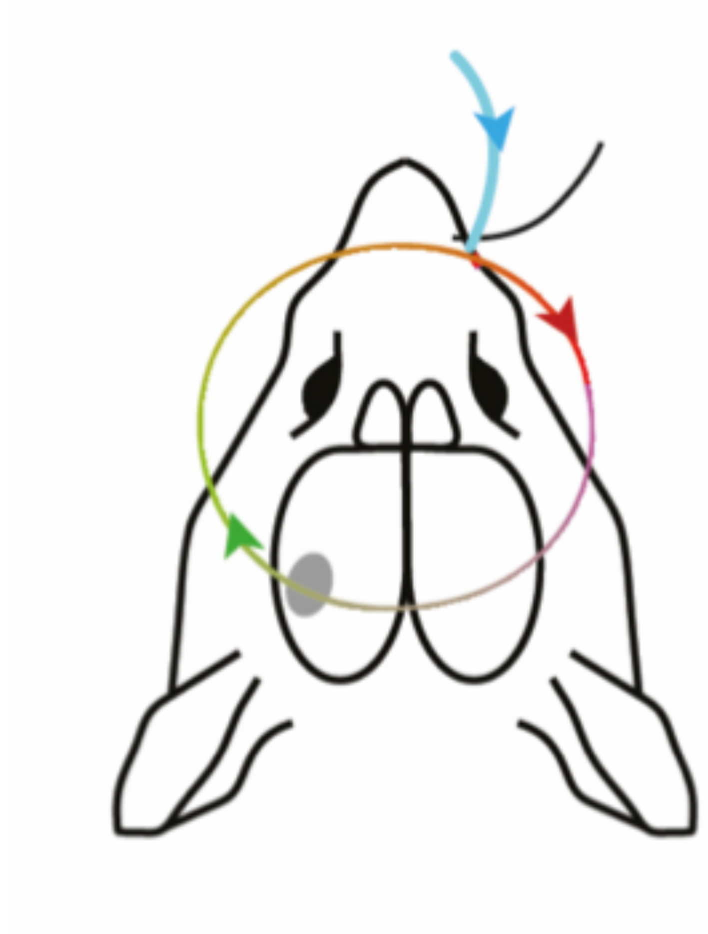
The model explains accentuated neural response to an active touch.

Sensory discriminability = Signal (evoked response) / Noise (Background membrane fluctuations)



Sensory feedback about whisker position is interrupted during the touch unless the whisker is too soft.
Neural gain transiently recovers during the touch, enhancing the sensory response.

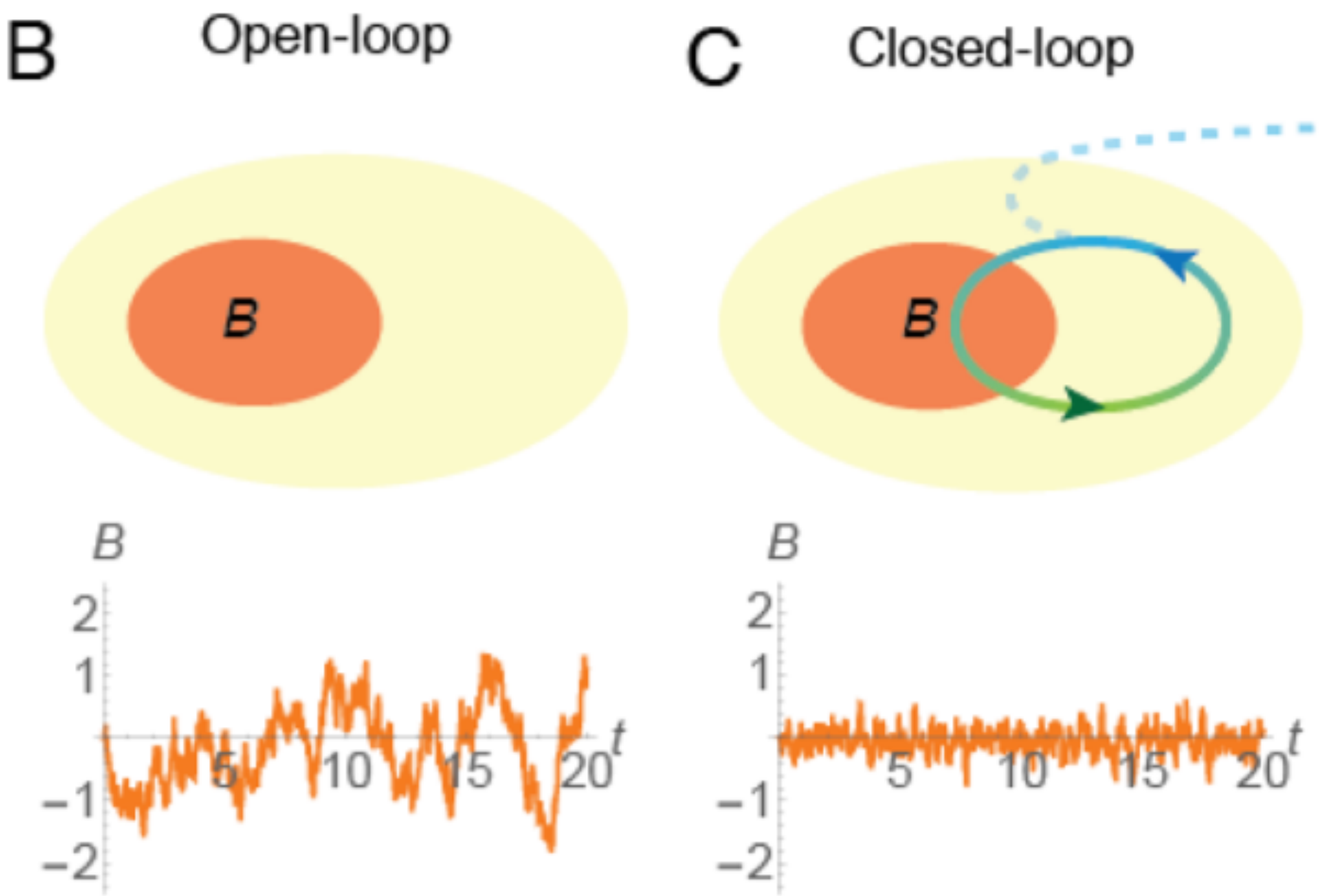
The model explains the observed changes in neural dynamics by a negative sensory feedback loop.



In contrast to the general predictive coding theory, neurons do not respond to unpredictable passive stimulation. It rather responds to interruption of sensory feedback.

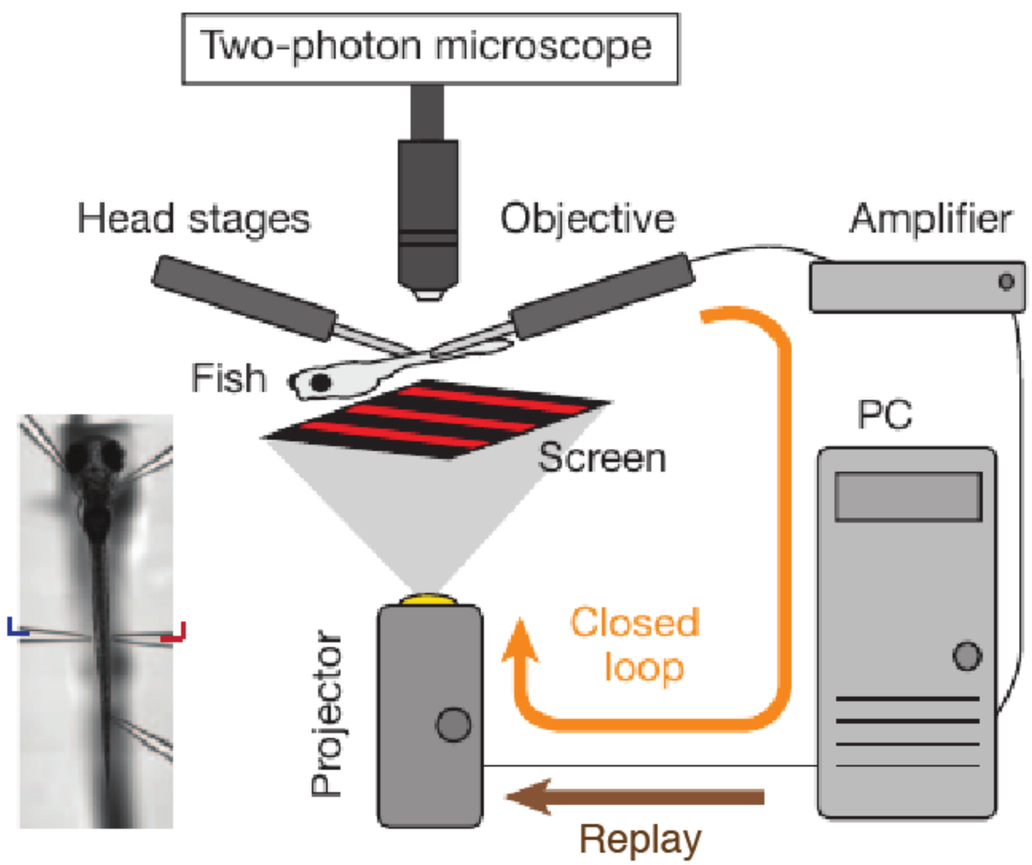
How to measure the effect of sensory feedback experimentally?

Testing the role of sensory feedback



The difference in neural activity between the closed-loop and replay conditions must be explained by the nature of the sensory feedback.

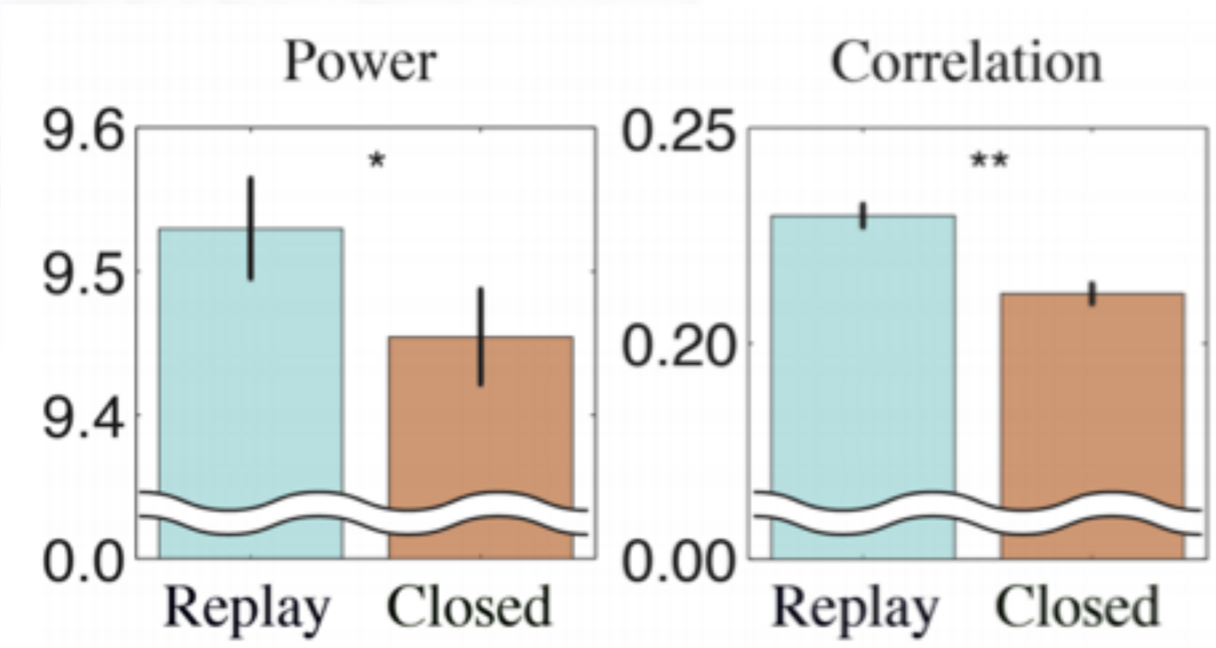
A virtual reality setup for larval zebrafish: Closed-loop vs replay conditions

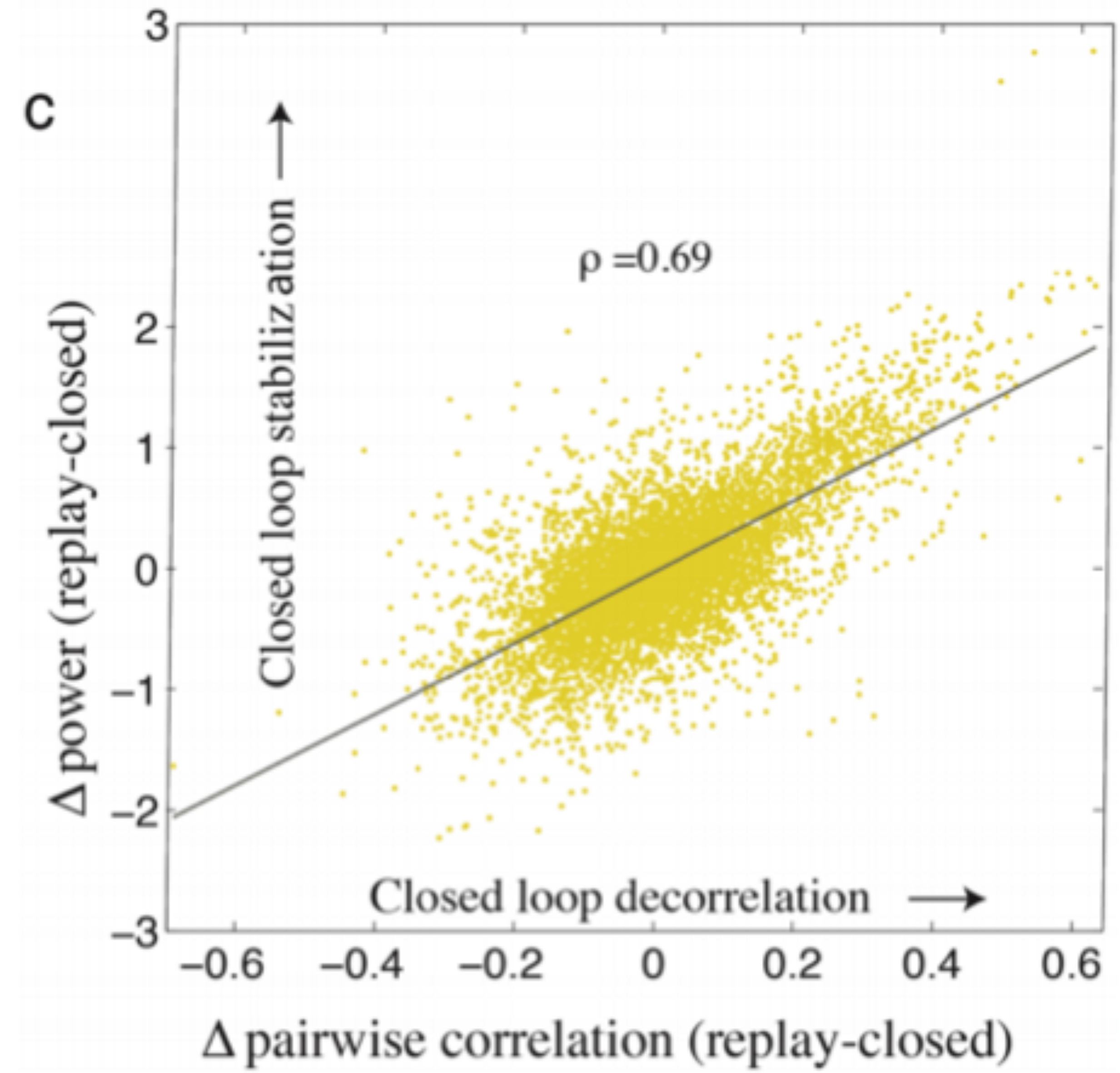


Ahrens et. al. 2012

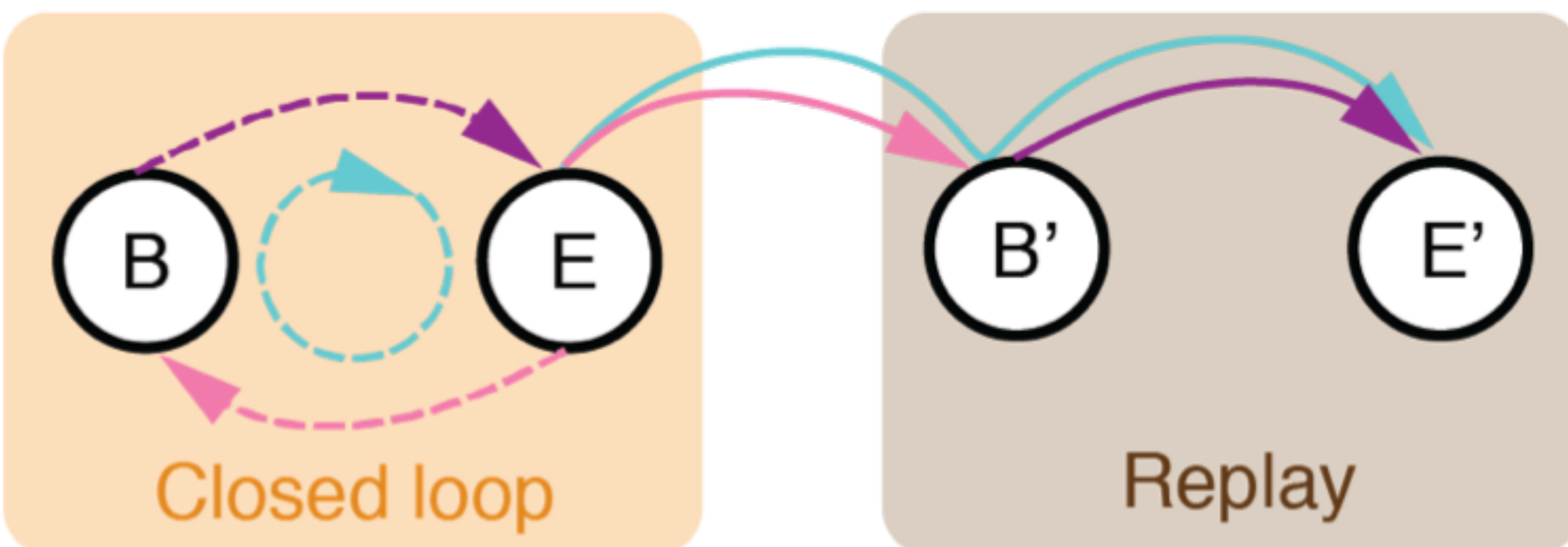
Closed-loop behavior modulated neural fluctuations and correlations. The net effect was suppression.

Average of all neurons



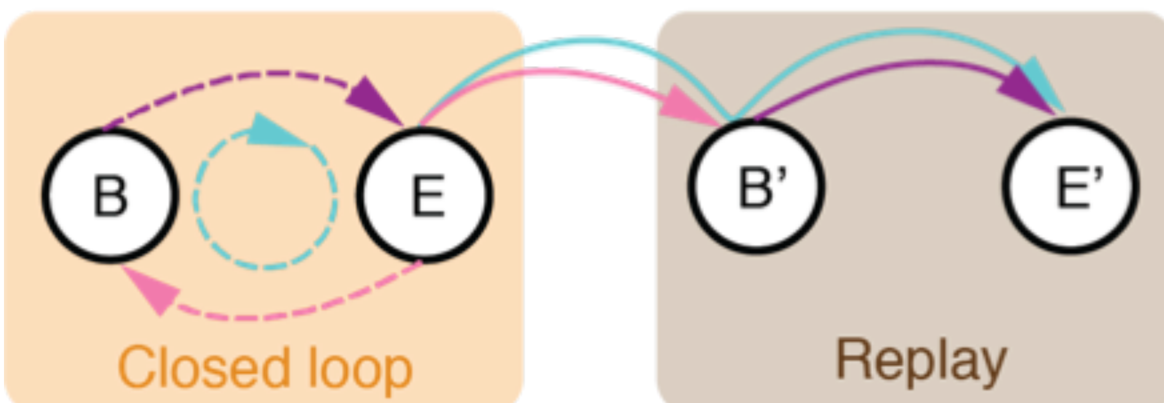


Estimating the strength of sensory feedback



B: Brain (neural activity)
E: Body/Environment (motor activity)

Estimated sensory feedback was negative.



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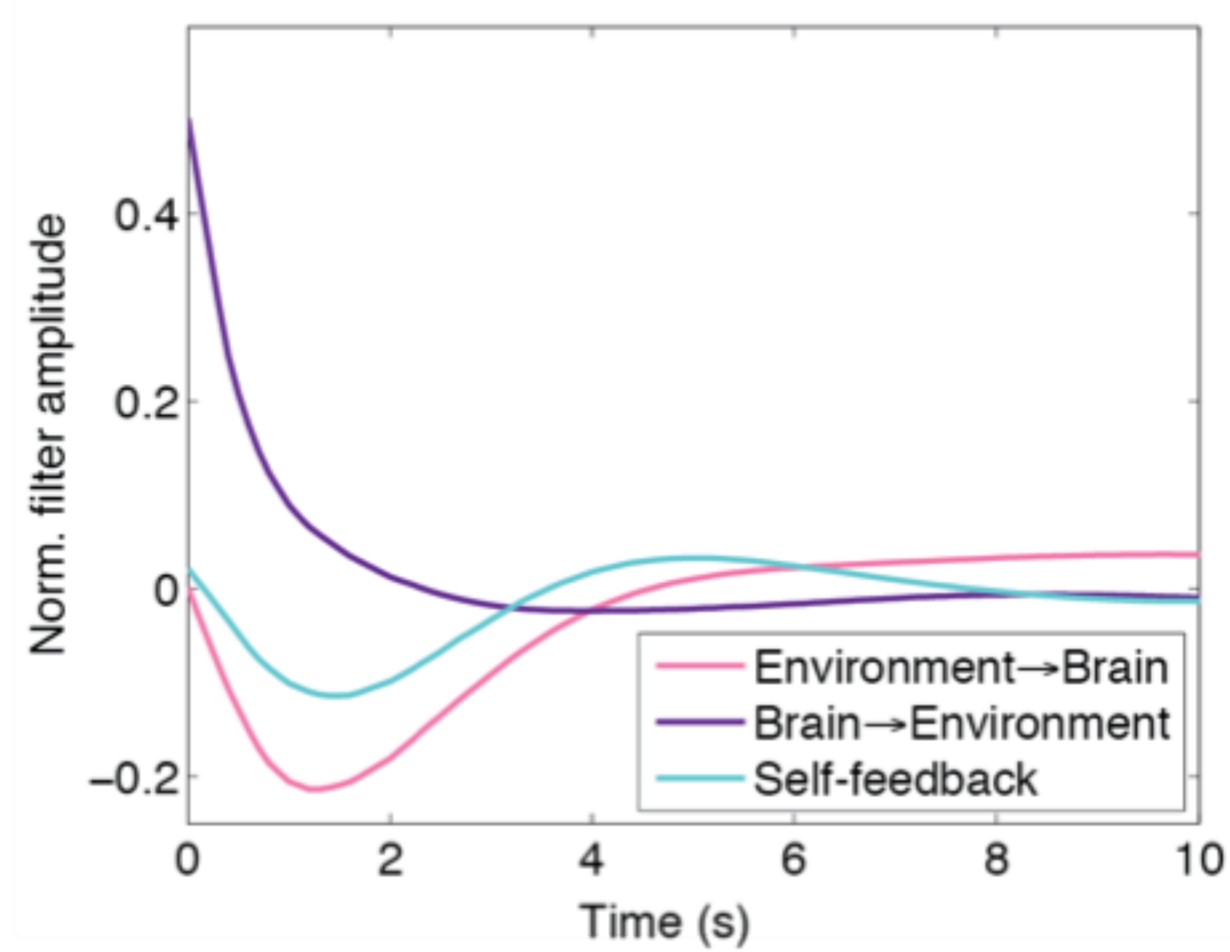
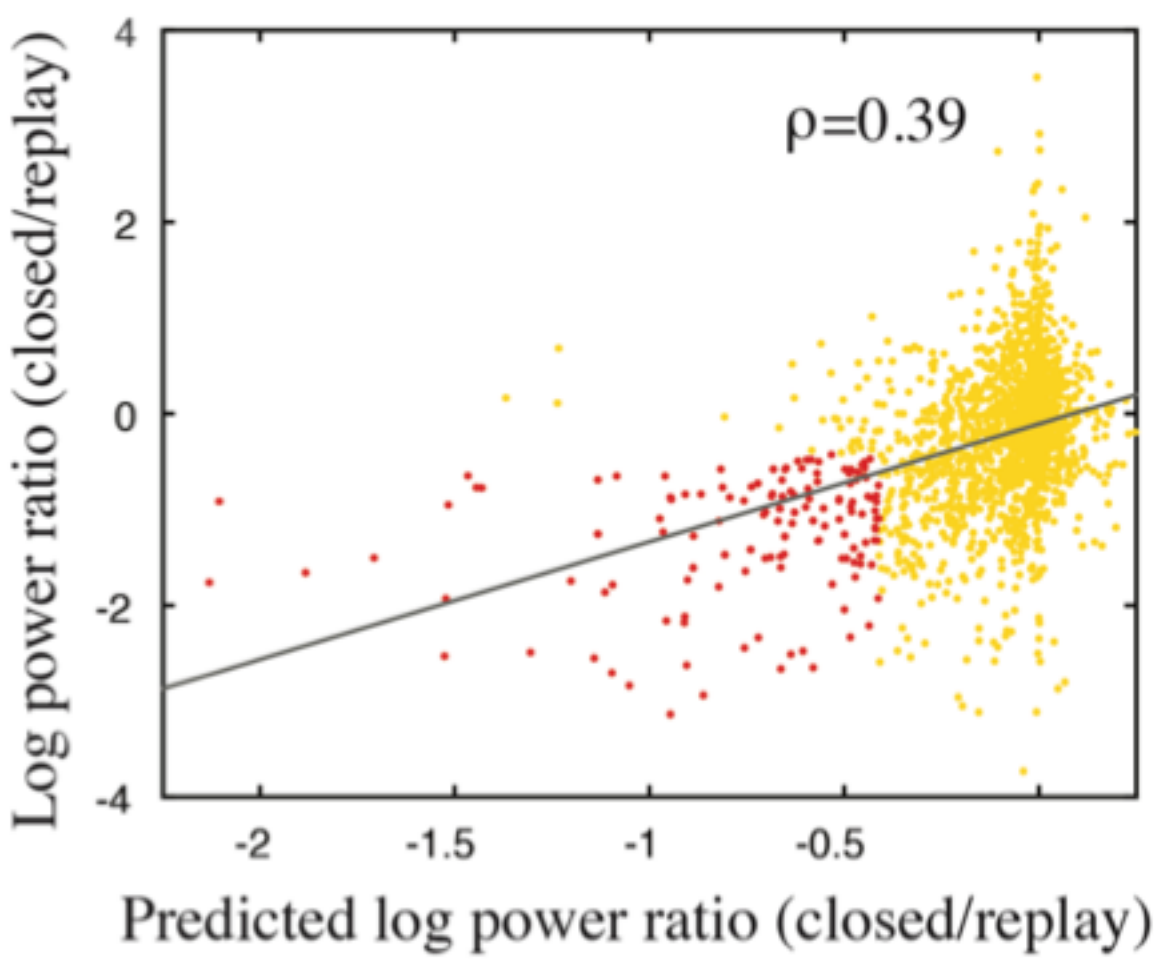
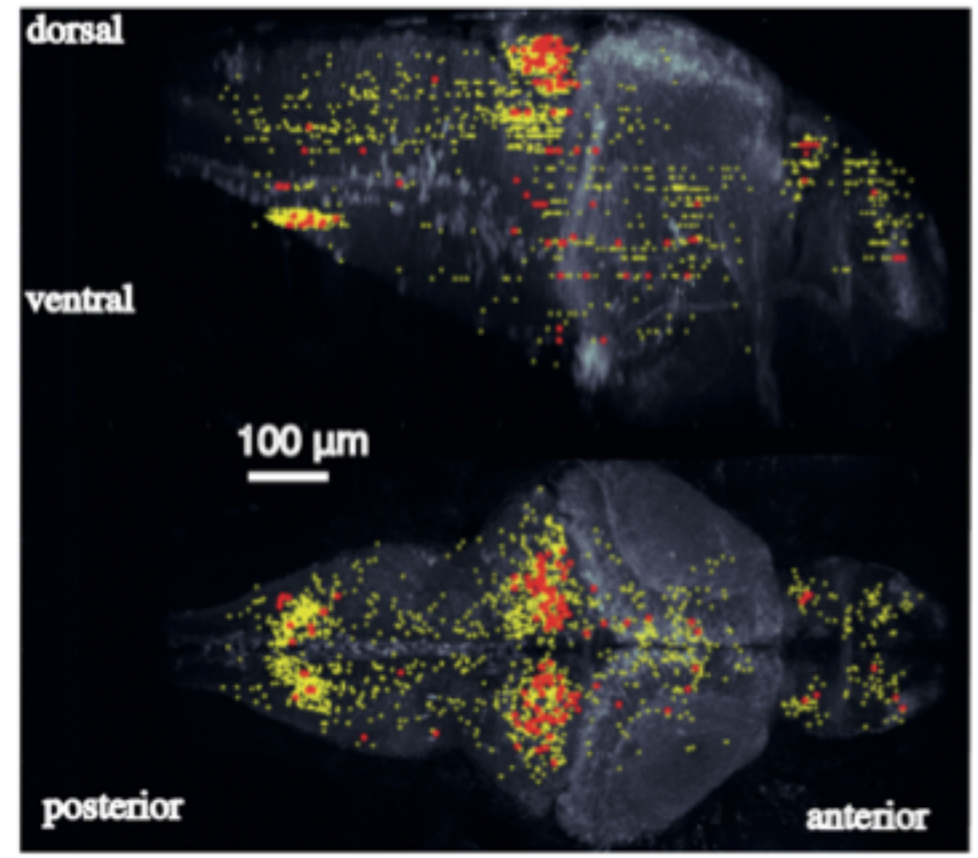


The strength of the closed-loop sensory feedback was correlated with the suppression of neural fluctuations.



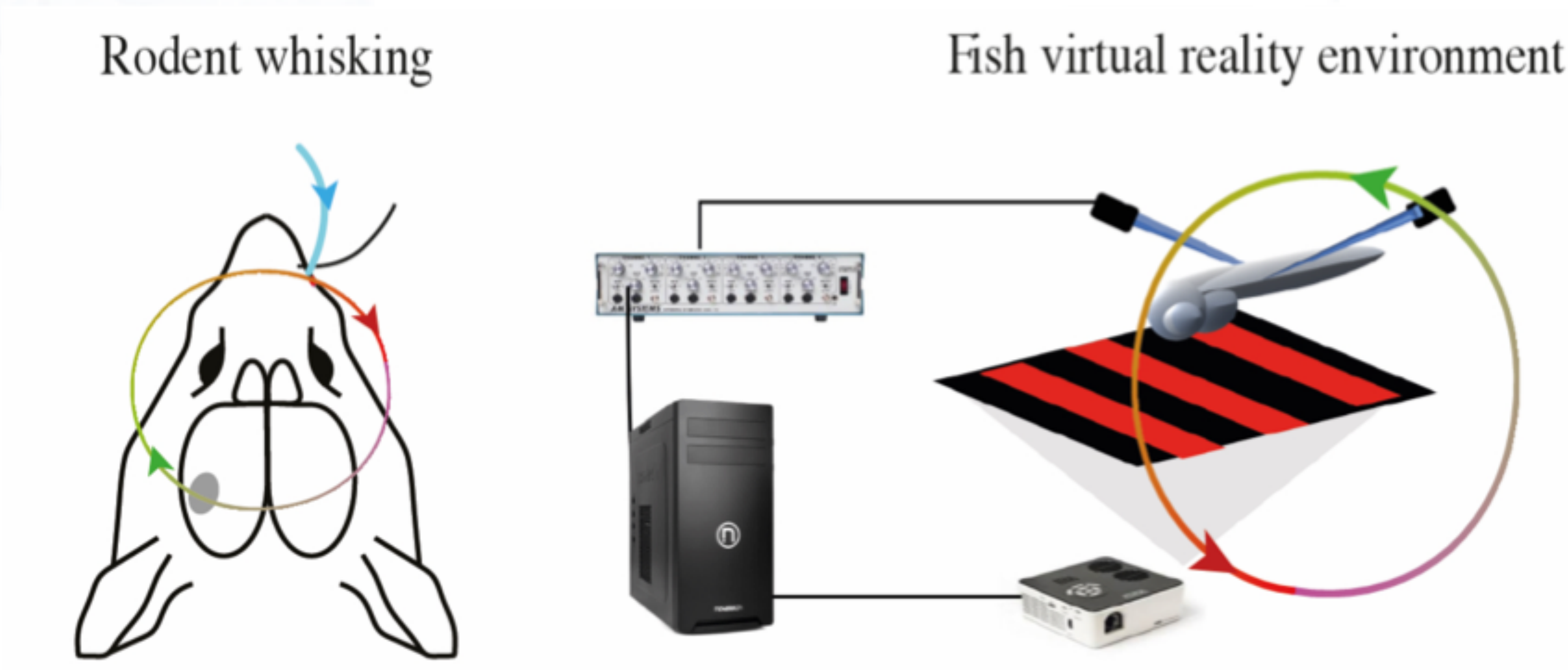


(Buckley and Toyoizumi 2018)

Top 10% feedback-suppressed-cells were clustered in the cerebellum, consistent with its role in opto-motor behaviors.

Summary

We have shown that the closed-loop sensory feedback has broad explanatory power for predicting coherent neural fluctuations in rodents and fish.



Discussion

- The barrel cortex does not respond to unpredictable passive whisker stimulation during whisking. Our theory suggests that neurons are sensitive instead to interruption of closed-loop sensory feedback.
- Brain dynamics during active perception cannot be fully recapitulated or re-encoded even if sensory input is precisely recorded and replayed into a passive brain.
- The proposed mechanism may shed light on how healthy and dysfunctional brain dynamics emerge from real-time brain/body/environment interactions. The artificial manipulations of these interactions may have medical and engineering applications.

We are not just our brains!

Collaborator

Christopher L. Buckley

(RIKEN BSI & Sussex U)

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