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Internal models and prediction errors

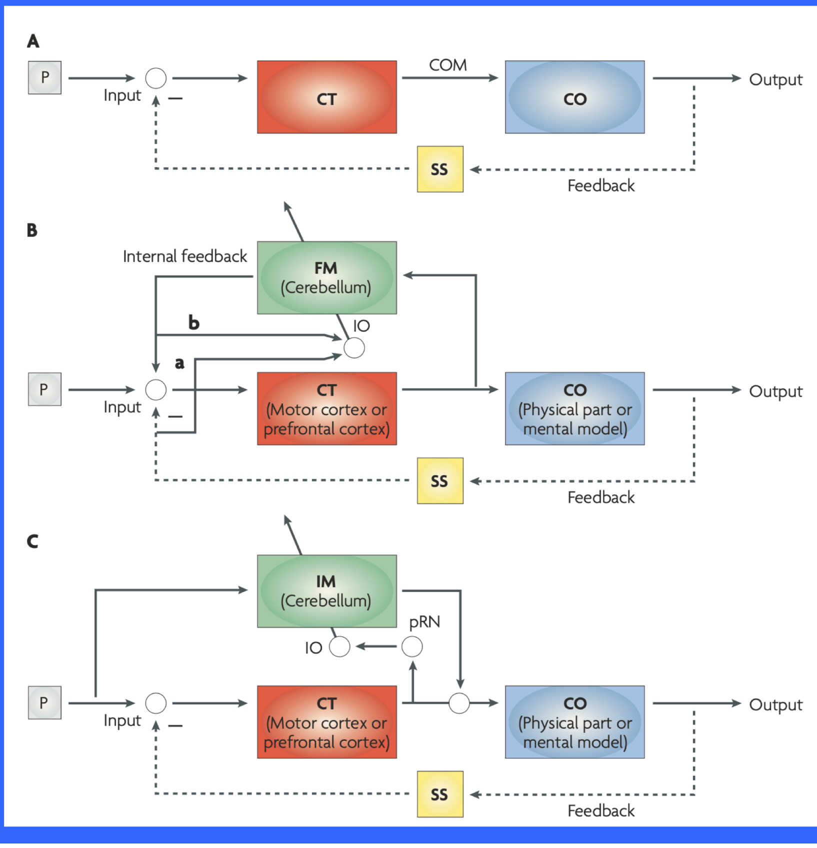
1. What are internal models?
2. Internal models for motor control
3. Internal models and the cerebellum
4. Non-motor functions of the cerebellum
5. Problems

1. Internal models

"Neural representations of our body or environment … how the brain interprets, predicts, and manipulates the world."
McNamee & Wolpert, 2019, Ann Rev Control Robot Auton Syst. 2: 339–364.

a) Models of statistical priors: statistical regularities of sensory inputs and the distributions of latent states
b) Perceptual inference models: computation of hidden "world states" given sensory input; conversely, generative models of the processes which generate sensory data.
c) Sensory and motor noise models: sensory and motor pathways are noisy, knowledge of which aids planning and implementing control policies
d) Cognitive maps, latent structure representation, and mental models: abstract relational structures between state variables
e) Forward and inverse dynamical models: see next

2: Internal models for motor control



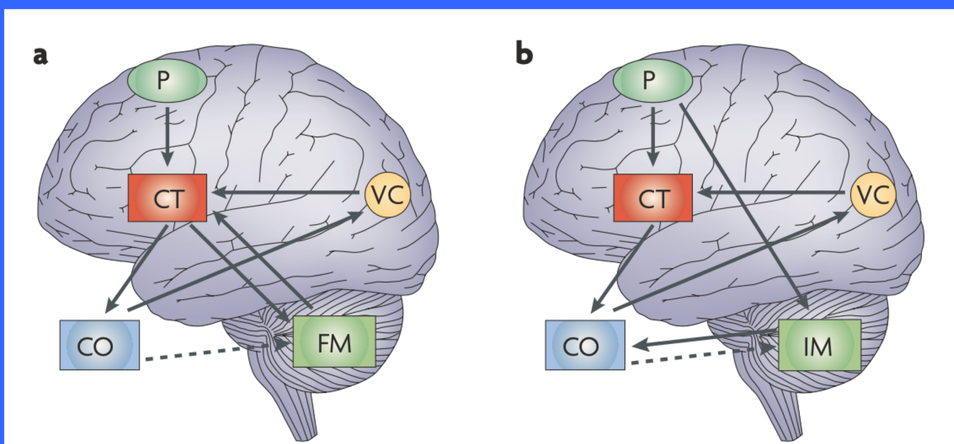
A. Control pathways: the motor system can be simplified to a controller sending commands to a controlled object. Each command moves the object into a new state. Feedback updates the controller to help achieve the desired plan

B. A forward model mimics the "forward process" from a command to a new state. This can provide an internal feedback signal avoiding sensory delays

C. A inverse model mimics the "reverse process" from desired state (a plan) to a motor command. This can provide automaticity, avoiding cortical processing delays

Ito, M. Control of mental activities by internal models in the cerebellum. *Nat Rev Neurosci* **9,** 304–313 (2008).

3: Cerebellar internal models

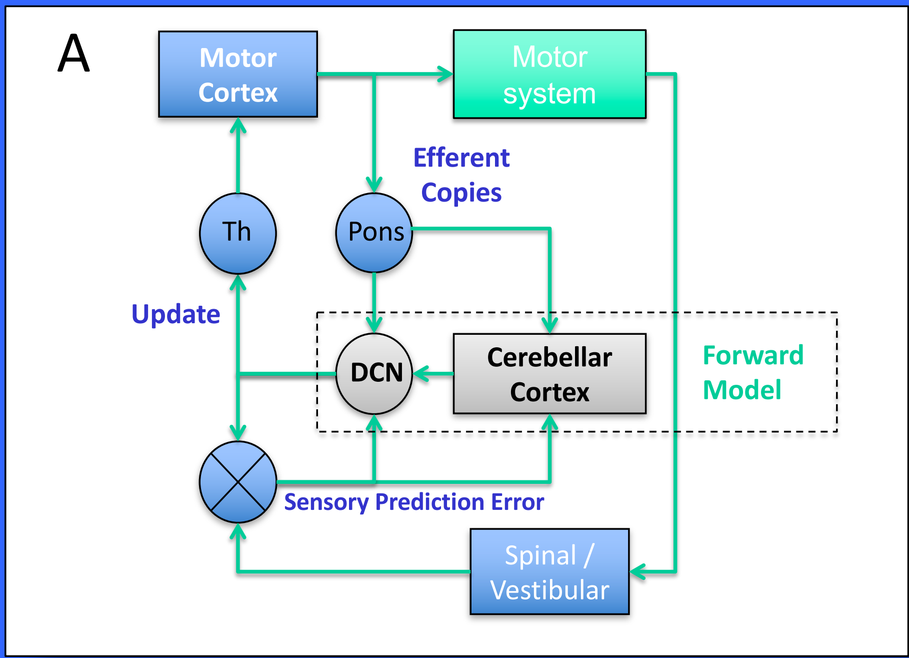


a: Cerebellar forward model mimics the forward process from motor command to sensory states, providing internal feedback.

b: Cerebellar inverse model bypasses motor cortical control to directly control the effector

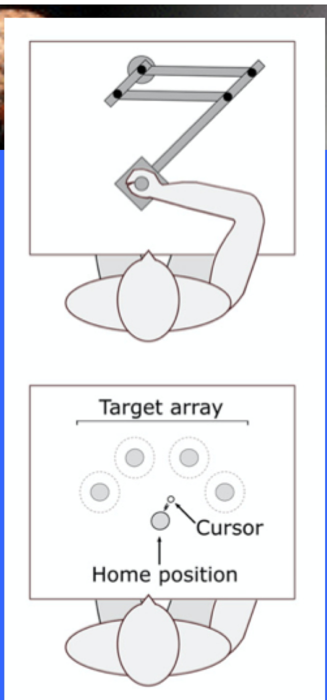
Ito M. (2008) Control of mental activities by internal models in the cerebellum. *Nat Rev. Neurosci* 9:304-313.

3: Cerebellar forward model & sensory prediction error



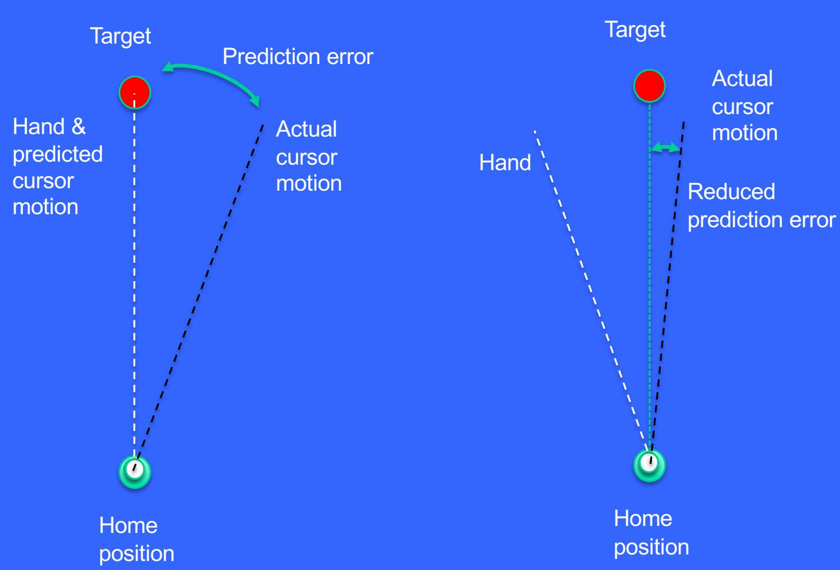
Sokolov, A. A., Miall, R. C. & Ivry, R. B. The Cerebellum: Adaptive Prediction for Movement and Cognition. *Trends in Cognitive Sciences* **21**, 313–332 (2017).

Prediction errors & visuo-motor adaptation



Before learning

Later in learning



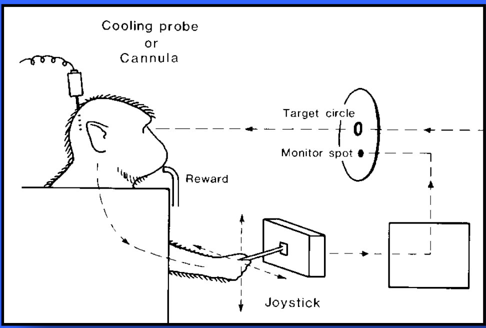
Galea, JM, Vazquez, A, Pasricha, N, Orban de Xivry, JJ & Celnik, P. Dissociating the Roles of the Cerebellum and Motor Cortex during Adaptive Learning. *Cerebral Cortex* **21**, 1761–1770 (2011).

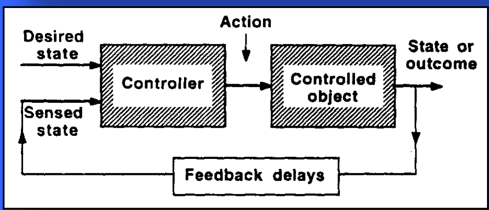
Taylor, JA, Klemfuss, NM & Ivry, RB. An Explicit Strategy Prevails When the Cerebellum Fails to Compute Movement Errors. *Cerebellum* **9**, 580–586 (2010).

Martin, TA, Keating, JG, Goodkin, HP, Bastian, AJ & Thach, WT. Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain* **119**, 1183–1198 (1996).

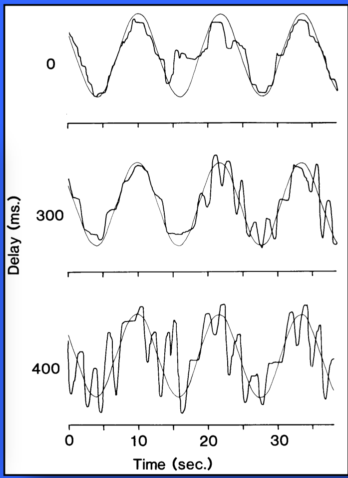
Sensory delays in feedback loops

1. Sensory feedback involves time delays
2. The cerebellum predicts the current state of motor system

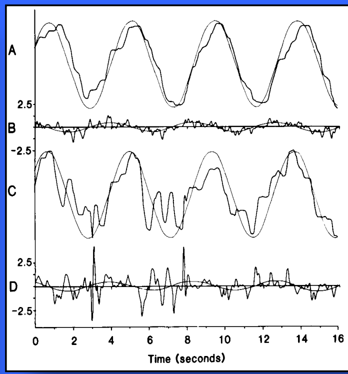




Delayed visual feedback

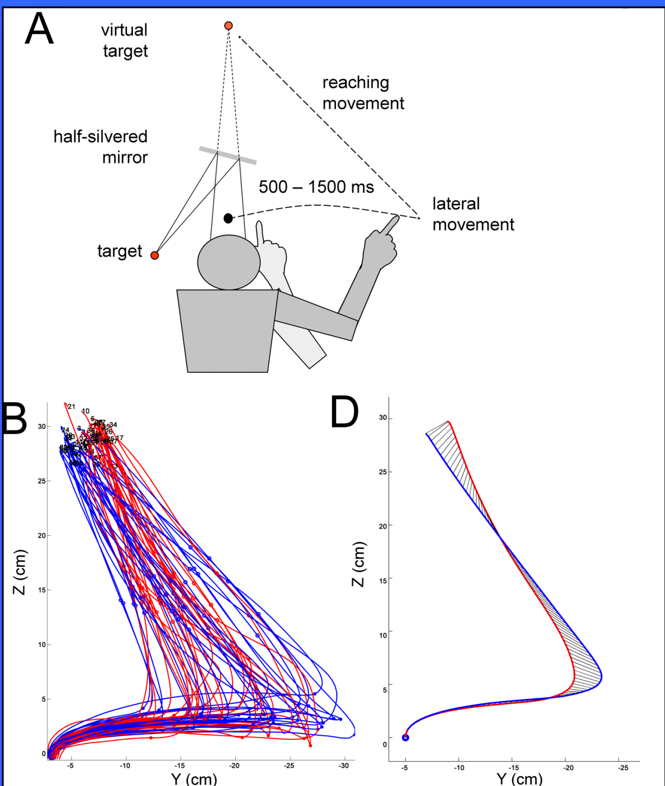


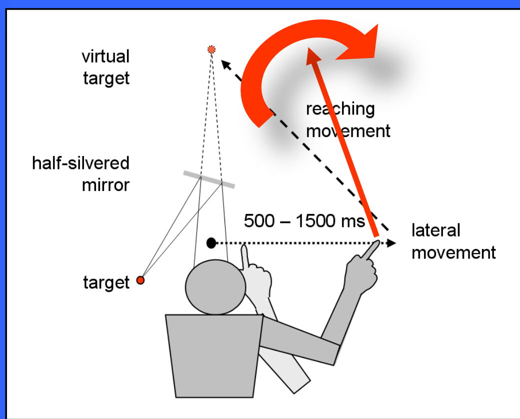
Cerebellar inactivation



Miall, et al. (1986) *Exp. Brain Res.*
Miall, et al. (1985) *Neurosci.*

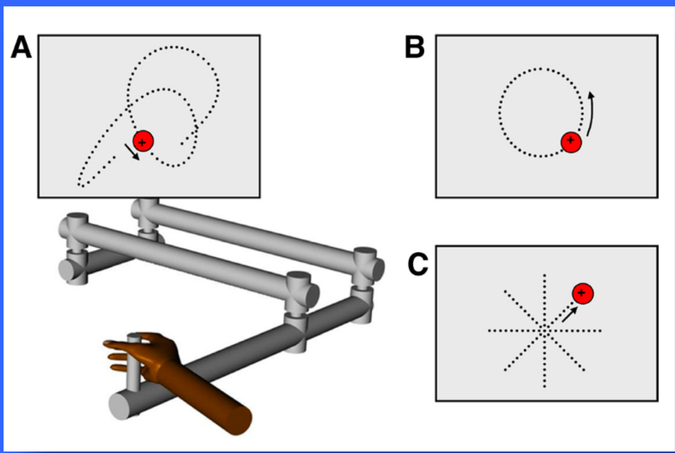
TMS disruption of cerebellar prediction

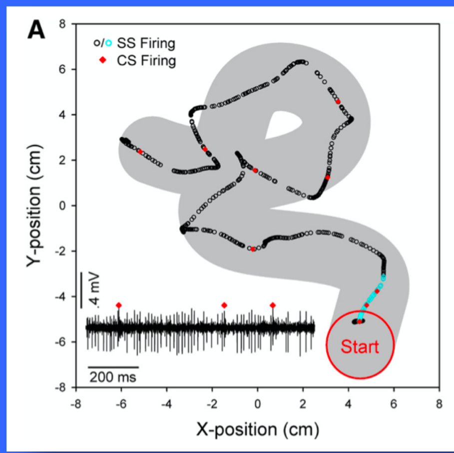


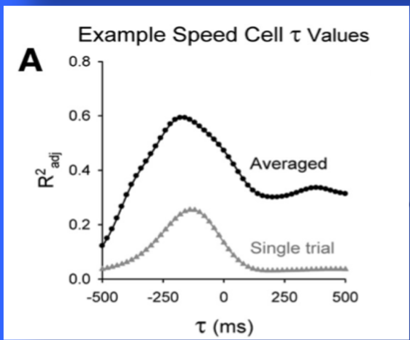


Miall, R. C., Christensen, L. O. D., Cain, O. & Stanley, J. Disruption of state estimation in the human lateral cerebellum. *PLoS biology* **5**, 2733–2744 (2007).

Representation of hand kinematics





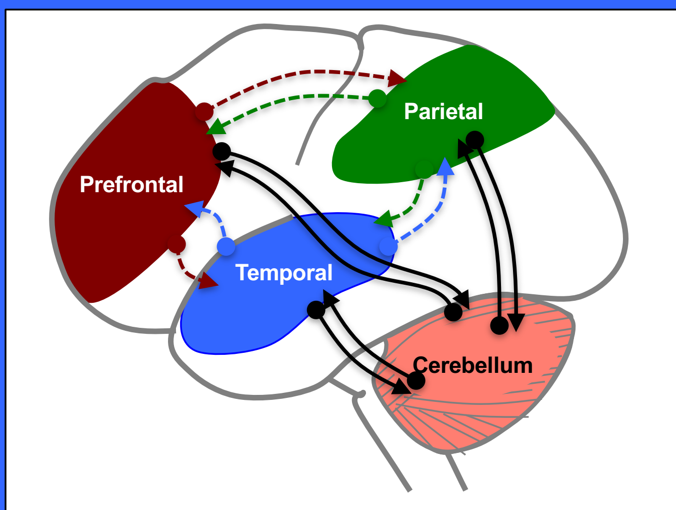


Across the population, velocity accounts for the majority of simple spike firing variability (63 +/- 30% of R^2), followed by position (28 +/- 24% of R^2) and speed (11 +/- 19% of R^2). Simple spike firing often leads hand kinematics.

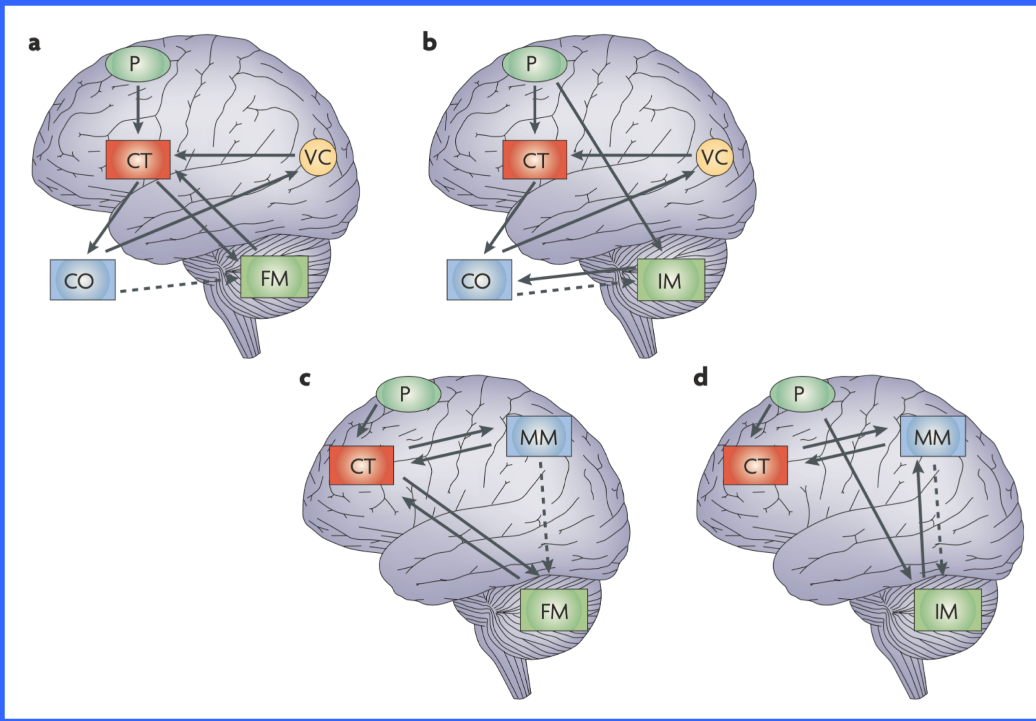
Hewitt, A. L., Popa, L. S., Pasalar, S., Hendrix, C. M. & Ebner, T. J. Representation of limb kinematics in Purkinje cell simple spike discharge is conserved across multiple tasks. *Journal of Neurophysiology* **106**, 2232–2247 (2011).

4: Non-motor cerebellar functions

- Is there just one cerebellar process?
- Prediction and state estimation …
- ...for motor functions
- ...for cognitive processes



Internal models for cognition



Ito M. (2008) Control of mental activities by internal models in the cerebellum. *Nat Rev. Neurosci* 9:304-313.

see also Ramnani N. (2006) The primate cortico-cerebellar system: anatomy and function. *Nat. Rev. Neurosci.* 7, 511-522

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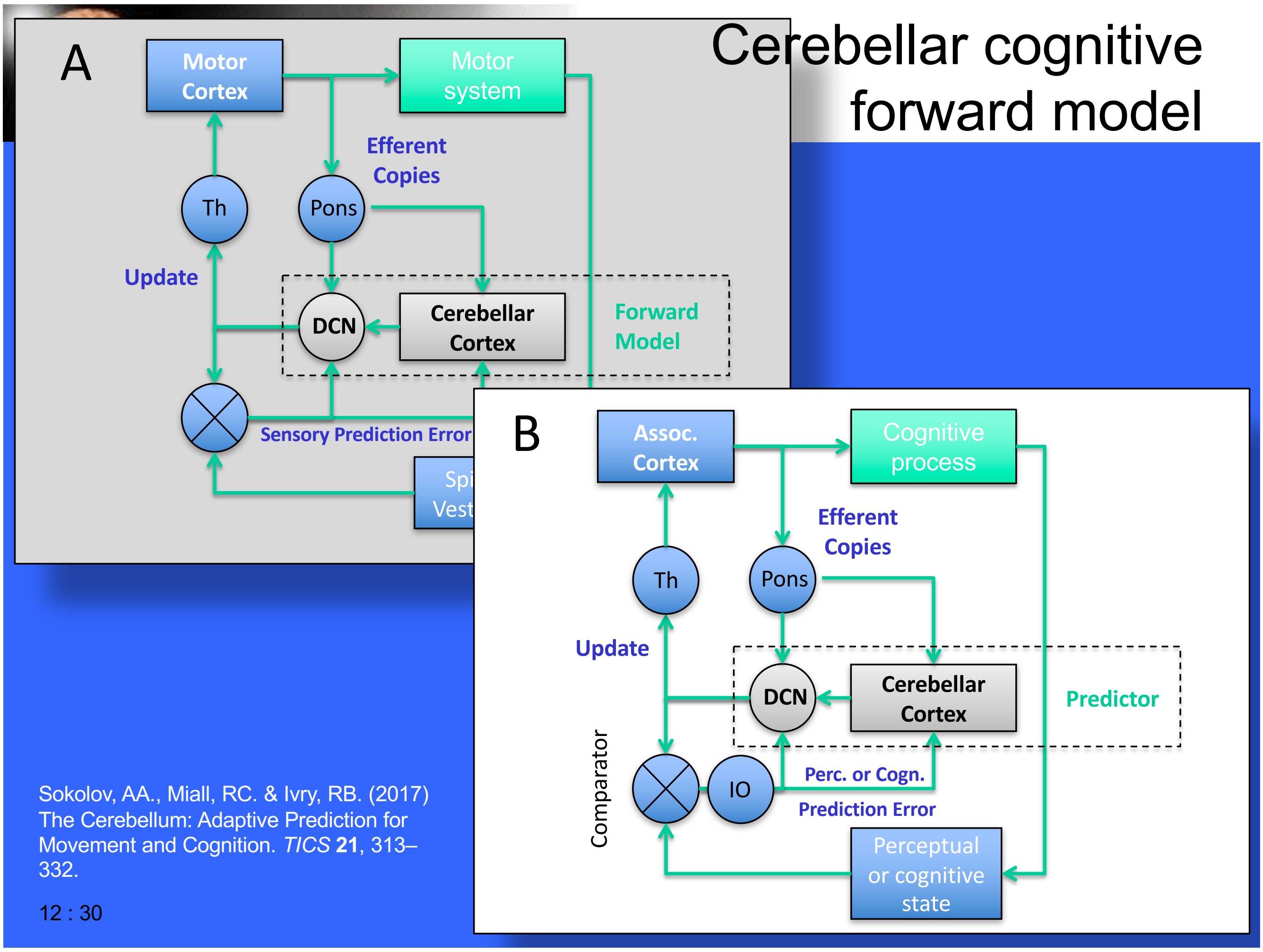
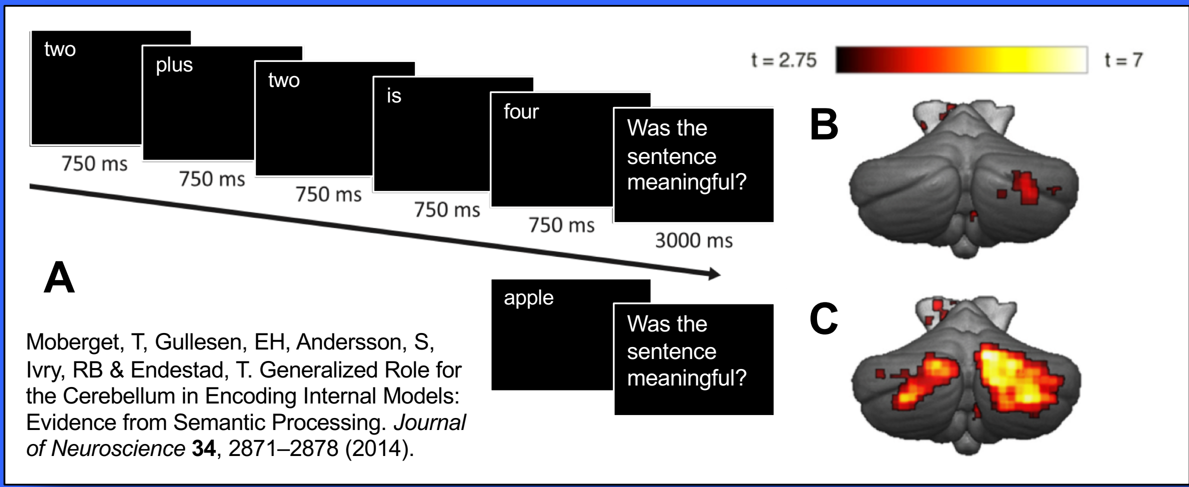
Cerebellar cognitive forward model



Sokolov, AA., Miall, RC. & Ivry, RB. (2017) The Cerebellum: Adaptive Prediction for Movement and Cognition. *TICS* **21**, 313–332.

12 : 30

Localizing language prediction



Moberget, T, Gullesen, EH, Andersson, S, Ivry, RB & Endestad, T. Generalized Role for the Cerebellum in Encoding Internal Models: Evidence from Semantic Processing. *Journal of Neuroscience* **34**, 2871–2878 (2014).

Sokolov, AA., Miall, RC. & Ivry, RB. (2017) The Cerebellum: Adaptive Prediction for Movement and Cognition. *TICS* **21**, 313–332.

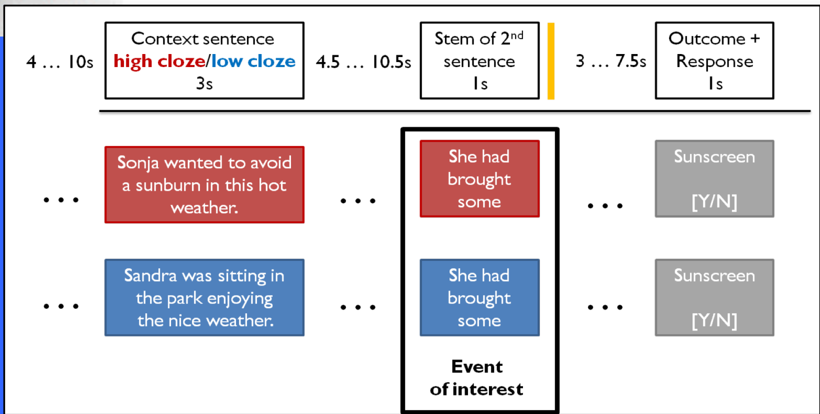
13 : 30

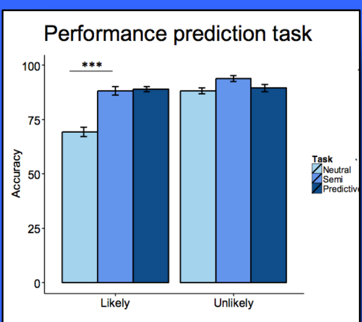
Localizing language prediction

Event related fMRI design with 3 events per trial

Subjects read the sentences, and made button response indicating plausibility of the outcome.

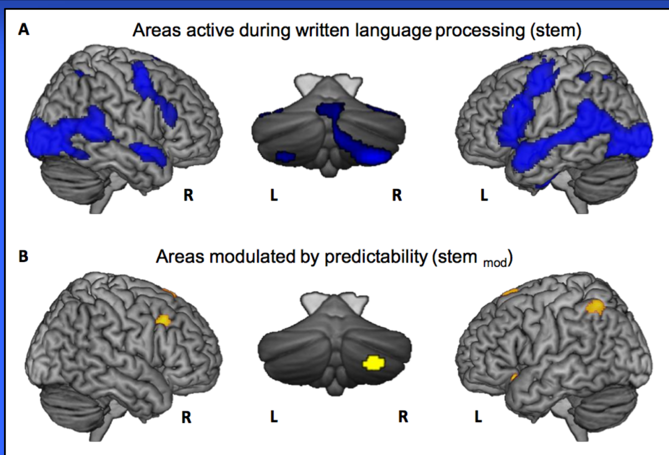
The STEM event did not require a motor response and was well-controlled for length and linguistic features.





Performance was high, except for neutral context trials

Lesage, Hansen, Miall, *J. Neurosci* (2017)

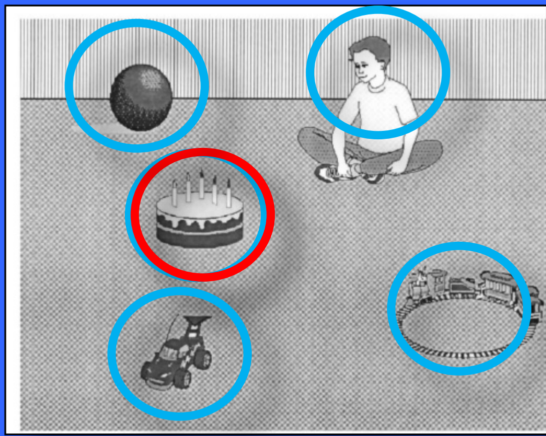


Disrupting linguistic prediction with TMS

- Visual world paradigm

  Altmann & Kamide (1999)

  - Participants listen to sentences whilst looking at a visual scene
  - Eye tracking to detect fixation on the target objects as spoken words are processed



"The boy will move the cake"

"The boy will **eat** the cake"

⇨ People predict future content "as they go"

⇨ We can use eye-movements to study these predictive processes

Disrupting linguistic prediction with TMS

Test group **R cerebellar rTMS**	vs	Control group I **No rTMS**	vs	Control group II **Vertex rTMS**

Significant interaction effect, as hypothesised:

- rm ANOVA 3-way interaction
- $F(2,62)=4.548$, **$p = 0.014$**).

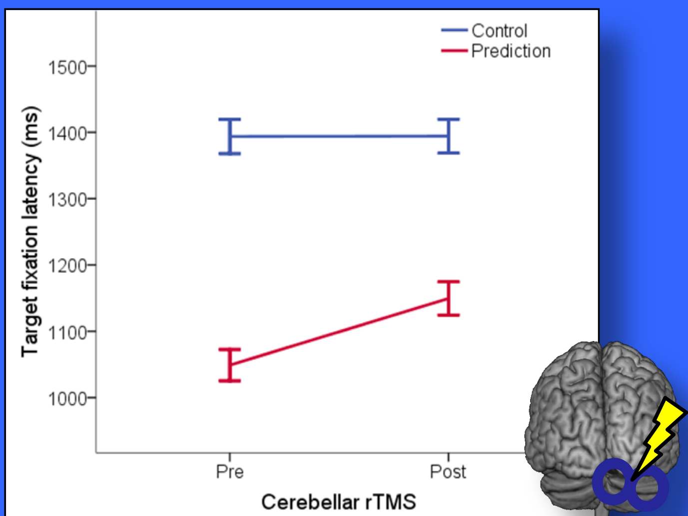
No differences in eye movement kinematics:

- average saccade velocity

  $t(21)=1.26$, $p=0.222$
- peak saccade velocity

  $t(21)=-0.04$, $p=0.972$
- saccade duration

  $t(21)=-1.64$, $p=0.116$



Lesage, Morgan, Olson, Meyer & Miall. *Current Biol* (2012)

5: Problems for forward model theory

- Evidence for inverse model (direct motor outputs:
  - Oculomotor control (VOR, saccadic control , smooth pursuit)
  - Eye-blink conditioning
- Mixed evidence for prediction:
  - Evidence for timing, sequencing, error correction
  - Purkinje cells codes not “clean” (Popa & Ebner)
  - Difficulty in understanding combined output of whole microzone onto cerebellar nuclear groups (Hertzfeld)
- Forward model should be trained by sensory prediction error (climbing fibres)
  - Timing signal (Llinas)
  - Reward prediction & reinforcement learning (Ohmae & Medina)

Conclusions

1. Predictive “forward models” are evident in sensory-motor pathways, and support coordination
2. Cerebellum contributes to the adaptive processes underlying prediction in motor and language domains
3. Understanding how the cerebellum functions requires deeper look at what complex spikes code, at the combined processing of a microzone population, and at the interactions with other brain systems – e.g. basal ganglia