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Contingency learning by an adaptive filter model of the cerebellum in simulated eyeblink conditioning

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N. Lepora is supported by BBSRC grant RA105089

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1 Introduction

Underlying question: Given the cerebellum is characterised by a uniform, repeating microcircuit, what *general* computation does it perform in adapting/controlling basic motor reflexes?

Exemplary model system: Eyeblink reflex

- Two main adaptive phenomena:
  - classical conditioning (*e.g.* to tone stimulus)
  - gain adaptation (*e.g.* to weighted eyelid to ensure blink closure)

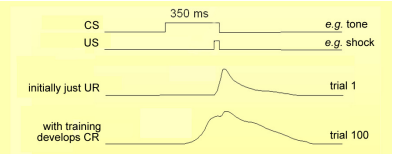
  Both depend critically on the cerebellum [Refs 1,2].
- Experiment: learning robust & tractable; depends on identified neuronal circuitry; emerging electrophysiological data.
- Modelling: well suited because non-complex movement; known simple model of eyeblink motor plant [Ref 3]; existing cerebellar motor control models, *e.g.* of vestibulo-ocular tracking reflex [Ref 4]

Modelling approach: Here we examine the computational role of cerebellum in classical eyeblink conditioning. In a companion poster we examined reflex blink adaptation [see Lepora et al 07, SFN 190.7].

2 Eyeblink conditioning

Classical conditioning of the eyeblink response.

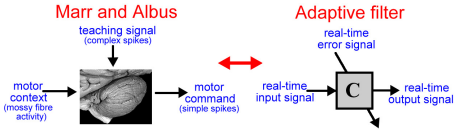
Terminology:
- **CS** – conditioned stimulus – behaviourally neutral, *e.g.* tone
- **US** – unconditioned stimulus – elicits response, *e.g.* shock
- **CR** – conditioned response – learnt blink to CS
- **UR** – unconditioned response – innate blink to US



- Cerebellar lesions produce loss of CR but not UR.
- Cerebellar complex spikes occur concurrently with US.
- Cerebellar simple spikes consistent with signalling blink motor command.

3 Computational hypothesis

The cerebellum implements an adaptive filter.
(Essentially a real-time version of Marr-Albus theory [Ref 5])



Note: cerebellar anatomy & adaptive filter structure also closely related (*e.g.* granule cell layer ↔ basis expansion; learning rule ↔ LTD/LTP).

- Input-output transformation adapts to remove any component of the output that correlates with the error signal – "decorrelation control" [Ref 4].
- Behavioural function of the cerebellar adaptive filter depends on its inputs, as determined by its mossy and climbing fibre afferents.

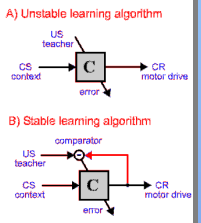
4 Problem: a stable end to learning

Key feature of classical conditioning: CRs do not affect the US
⇨ problem applying adaptive filter model to classical conditioning.

Map CS & US onto Marr-Albus model (Fig A)
But if the CR cannot affect the US
⇨ US error signal never driven near zero
⇨ adaptation never ceases - unstable.

Anatomically: US → cerebellum via olive.
Olive has two inputs:
i) excitatory US;
ii) inhibitory feedback from cerebellar output (Fig B).

Comparator model of olive [Ref 6] allows for stable learning: gating the US with an inhibitory copy of the CR drive is an error that can become zero upon learning completion.



5 Model of eyeblink conditioning

Include a non-adaptive unconditioned reflex pathway in parallel with an adaptive conditioned reflex pathway.

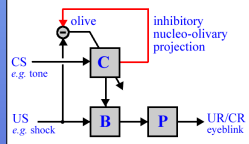


Fig. The CS inputs to the cerebellum could correspond to *e.g.* a tone reliably presented before a shock US.

US→UR pathway through brainstem B gives unconditioned reflex in absence of cerebellum.

CS→CR pathway through cerebellum C gives conditioned reflex upon CS presentation. Converges with US→UR pathway at premotor nuclei in B.

CR acquisition driven by comparator error from gating the US with an inhibitory copy of CR motor drive.

(See technical appendix for definition of model components & assumptions.)

6 Results: CR acquisition & extinction

Robust and stable learning of a conditioned response (CR)
CR acquisition – increase of CR peak amplitude over paired CS-US trials;
CR extinction – decrease of CR peak amplitude over CS-alone trials.

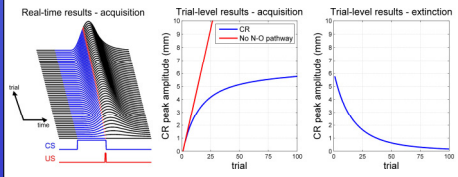


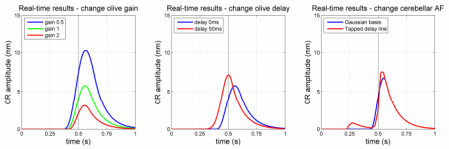
Fig. Real-time results – changing response profiles from trial to trial;
Trial-level results – just the change in CR peak amplitude from trial to trial.

- **Stability**: Nucleo-olivary projection required for stable learning – absence of N-O projection causes instability (shown in red on plot; consistent with arguments on slide 5)

7 Results: Arbitrary CR profile

However, the CR profile depends on model parameters:
- Gain term in plant or olive – changes CR peak amplitude.
- Delay term in olive – changes CR peak timing.
- Change cerebellar basis filters – changes shape of CR.

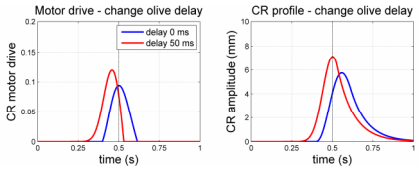
(See technical appendix for details of these changes to basic model.)



Important note:
- Trial-level results (for CR peak amplitude) for acquisition and extinction learning curves are *robust* to these changes (up to an overall change of amplitude scale).

8 Observation: Olive delay & plant delay

Problem from having a visco-elastic plant:
- Visco-elastic plant ⇨ CR peak delayed ~50ms after CR motor drive peak
- But olive comparator ⇨ CR motor drive peak timed to US
  Therefore CR peak too late (blue plot). Not seen experimentally.



Arbitrariness of the model CR profile provides a solution:
- Delay in olive comparator ⇨ CR motor drive peak timed earlier than US
  Therefore CR peak can be correctly timed to US (red plot).

Consistent with observed nucleo-olivary synaptic time const ~50ms.

9 Extend model to contingency learning

Include multiple conditioned stimuli (CS) inputs to cerebellum.

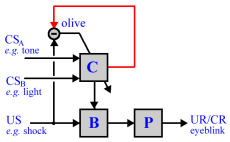


Fig. Multiple CS inputs to the cerebellum could correspond to *e.g.* a tone and a light presented reliably before a shock US.

Can then examine following effects:

Blocking:
When a CR is learned to CS_A it blocks CR learning to a second stimulus CS_B.

Overshadowing:
When a CR is learned to a compound CS, the CR to each CS component is diminished (compared to if it had been trained alone) and the more salient CS dominates.

Conditioned inhibition:
If CS_A reliably predicts the US and CS_A+CS_B reliably predicts no US, then CS_B acquires an inhibitory property. Inhibition is manifest by, *e.g.* extended training required to acquire an overt CR to CS_B.

10 Results: Robust contingency learning

Adaptive filter (AF) model naturally learns contingencies between multiple conditioned stimuli.

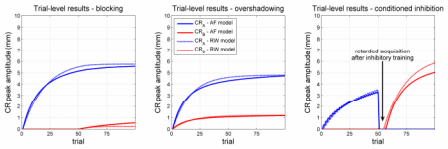


Fig. Trial-level results – change in CR peak height from trial to trial.
Plots show the individual CRs to CS_A and CS_B after appropriate training.

Important features:
- Trial-level results identical to Rescorla-Wagner (RW) model (dashed lines).
- Results are *robust* to changes of model parameters discussed on panel 7.
- **Interpretation**: the AF covariance learning rule applied to comparator error (see technical appendix) is similar mathematically to the RW learning rule. Hence the AF model learns contingencies, robustly to changes of the model.

11 Conclusions

Summary:
- Applied generic adaptive filter version of Marr-Albus model of the cerebellum to eyeblink conditioning.
- For learning stability the US cannot be the error signal; we use a comparator model of the olive that gates the US with inhibitory copy of cerebellar output.
- For a single CS, this model produces stable CR acquisition and extinction.
- Trial-level results are robust, but CR profiles depend on model parameters.
- For multiple CSs, the AF model naturally exhibits robust contingency learning. Results are consistent with the Rescorla-Wagner model.

Implications:
- The adaptive filter model of the cerebellum applies to prediction (including contingency effects), in addition to its applicability for motor control [Ref 4].
- This approach draws together features from previous models of eyeblink conditioning [*e.g.* Refs 7 & 8], and demonstrates that contingency learning follows from the covariance learning rule with a comparator error signal.

References

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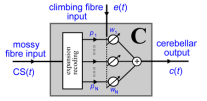
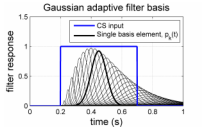
12 Appendix: Technical details

Adaptive filter (AF) model:
Input-output transformation
$c(t) = \Sigma_k w_k p_k(t)$, $p_k(t) = G_k[CS(t)]$,
with a covariance learning rule
$\delta w_k = -\beta\, e(t) p_k(t)$.

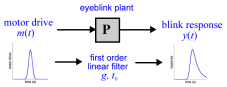


Gaussian adaptive filter basis:
Basis filters G_k transform $CS(t) \to p_k(t)$.
For CS that is a rectangular pulse, use filters giving a gaussian basis. (Note: nonlinear filters.)



Brainstem model:
Model as signal addition, $m(t) = US(t) + c(t)$.

Motor plant model:
Known to be first order filter [Ref x]
i.e. $\dot{y}(t) - y(t)/t_0 = g\, m(t)$
with gain g, time const t_0~100ms.
Note: Plant model based on nictitating membrane, which has no antagonist.
⇨ truncate $c(t) \geq 0$ to ensure $m(t) \geq 0$.



Olive model (with delay):
Comparator between US and CR motor drive
$e(t) = US(t) - g\, c(t-t_d)$
including a N-O delay t_d and gain g.