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A computational model of adaptive blink modification by the cerebellum

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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:
  - reflex blink adaptation (to weighted/counterweighted eyelid)
  - classical conditioning (e.g. to tone stimulus)

  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 "control" models, e.g. of vestibulo-ocular tracking reflex [Ref 4]

Modelling approach: Here we examine the computational role of cerebellum in adaptive blink modification. In a companion poster we examine classical conditioning [see Lepora et al 07, SFN 636.11/DDD28].

2 Reflex blink adaptation

Counterweight or restrain eyelid ⇨ amplitude of reflex blink (*e.g.* to airpuff) gradually adapts to ensure correct blink completion.

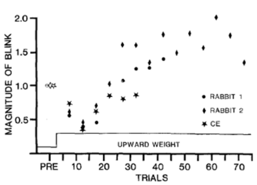
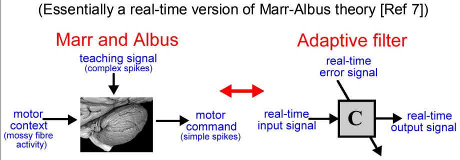


Fig. Adaptation of two rabbits and one human to upwardly directed force on the upper eyelid. Normalised blink amplitude (mean of 20 preweight trials normalised to 1.0) a function of trial number, and averaged over 5 trials (plot from [Ref 5]).

- Cerebellar lesions prevent adaptive gain change in blink reflex [Ref 1].
- Adaptation related changes of neuronal activity in the cerebellar cortex and deep nuclei are consistent with a cerebellar role [Refs 5 & 6].

3 Computational hypothesis

The cerebellum implements an adaptive filter.
(Essentially a real-time version of Marr-Albus theory [Ref 7])



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 Model of reflex adaptation

Include an adaptive pathway through the cerebellum in parallel with the unconditioned reflex pathway through the brainstem.

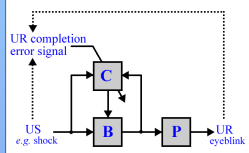


Fig. The US inputs the brainstem directly, and inputs the cerebellum via direct & recurrent pathways.
A typical US is *e.g.* periocular shock.

US→B→UR pathway through brainstem gives unconditioned reflex in absence of cerebellum. Consider to be non-adaptive.

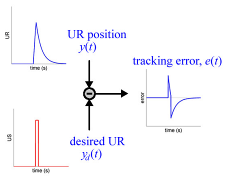
US→C→UR pathway through cerebellum contributes to UR size, but not needed for UR initiation. Converges with US→B→UR pathway at premotor nuclei in B.

Cerebellar contribution to US→UR reflex is adaptive, with adaptation driven by error signal of UR completion.

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

5 UR completion error – tracking error

A leading choice for UR completion error is tracking error.
Tracking error is believed to be the cerebellar input for controlling accuracy in some reflexes, *e.g.* vestibulo-ocular reflex.



Define tracking error:
Suppose the US gives a desired lid position
$y_d(t) = y_0$, US(t) on, (*i.e.* close lid)
0, US(t) off, (*i.e.* open lid)
where y_0 (*e.g.* 10 mm) is the complete blink amplitude for the fully closed lid.

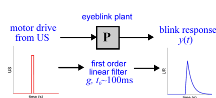
Tracking error is the difference between actual $y(t)$ and desired $y_d(t)$ lid positions
$e(t) = y(t) - y_d(t)$.

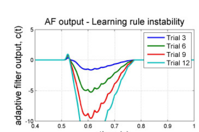
6 Problem – error instability

Tracking error cannot be driven to zero for the blink reflex ⇨ instability because the system never stops learning.

Non-trivial eyeblink plant dynamics imply the UR can never match the US, *e.g.*
1) initial UR is later than US onset by the time the system takes to respond,
2) if the UR tail is a passive movement (as for the nictitating membrane, which has no antagonist), then any UR after US offset cannot be driven to zero.

If the UR & US cannot match, the tracking error remains non-zero. This keeps driving learning in the cerebellar adaptive filter model, which leads to instability.





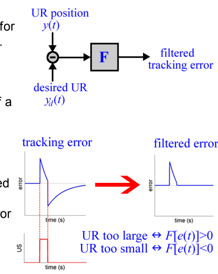
7 Possible solution – error filtering

The above error instability is known to occur for some plants; for example, when the plant has an improper inverse (*e.g.* from delays).

There are a number of general methods for stabilising control in these situations; *e.g.* filtering the error signal to remove the component driving the instability.

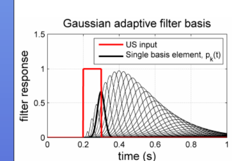
Here we consider one simple example of a filtered error: US-gated tracking error
$e(t) = y(t) - y_d(t)$, $US_{on} \le t \le US_{off}$
0, otherwise.

This error signal is consistent with the cerebellar complex spike activity observed for saccadic adaptation [Ref 8], which appears to signal end-point error (the error at the end of the movement).



8 Other constraints from error filtering

We found that error filtering only gives realistic URs if the cerebellar adaptive filter is tuned appropriately.
This is a general implication of error filtering, because there will be components of the output not controlled by the error signal.



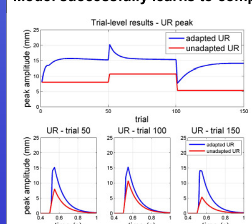
Adaptive filters produce their outputs from a linear combination of basis functions (see technical appendix for mathematical details; biologically, the basis functions correspond to parallel fibre activity).

Gaussian basis functions were sufficient to give an adaptive filter output that resulted in a realistic shaped UR (see following slide).

Note: to ease implementation in this pilot study we restricted ourselves to the forward architecture in slide 4, although we expect suitable basis functions can also be found for the recurrent architecture.

9 Results – reflex adaptation

Model successfully learns to compensate changes in plant gain.



Plant gain changes to 4/3 of its initial value at trial 50, then 2/3 of its initial value at trial 100.

Top Fig. UR peak amplitude (blue) as it adapts to a changing plant. Unadapted UR also shown (red) for just the brainstem pathway.

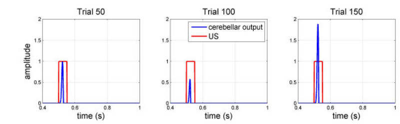
Bottom Figs. Adapted (blue) & unadapted (red) UR profiles on trials 50, 100 & 150.

Note: The unadapted UR is smaller than the adapted UR because the model up and down-modulates the excitatory cerebellar drive. This is consistent with inactivation of cerebellar output decreasing UR amplitude [Ref 9] .

10 Results – cerebellar output

Model UR adaptation achieved by modulating cerebellar output, which combines with the direct US drive to modulate the UR motor drive.

Simulation leads to a stable cerebellar output that up and down-modulates its amplitude while remaining timed to US onset.



Further work: needed to investigate the relation to deep cerebellar nuclei firing in blink reflex adaptation. Some evidence for a change in cerebellar output duration, rather than amplitude, to modulate blink amplitude [Ref 6]. If confirmed, this could relate to the error filter or AF basis (slides 7 & 8).

11 Conclusions

Summary:
- Applied generic adaptive filter version of Marr-Albus model of the cerebellum to reflex blink adaptation.
- The model architecture consisted of a non-adaptive brainstem pathway and a parallel adaptive cerebellar pathway, converging on premotor nuclei.
- For a tracking error between the actual UR and a desired UR (defined by the US) this model was unstable when learning fails to drive the error to zero.
- However, a filtered error signal (US-gated tracking error, or end-point error) gave stable results. The model then achieved successful blink modification to compensate for changes in eyeblink plant gain.

Implications:
- Cerebellar role in blink adaptation can be modelled with an adaptive filter architecture, provided appropriate error information is available.
- This result illustrates the importance of obtaining direct experimental evidence for the error signal, especially as end-point error is very similar to the signal proposed for saccadic adaptation [Ref 8].

References

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12 Appendix: Technical details

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

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

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. $\dot{y}(t) - y(t)/t_c = g\, m(t)$
with gain g, time const t_c~100ms.
Note: Plant model based on nictitating membrane, which has no antagonist.
⇨ truncate $c(t) \ge 0$ to ensure $m(t) \ge 0$.