

# Visual awareness and the cerebellum: possible role of decorrelation control

Paul Dean\*, John Porrill and James V. Stone

*Department of Psychology, University of Sheffield, Western Bank, Sheffield S10 2TP, UK*

**Abstract:** The two roles in awareness most often suggested for the cerebellum are (i) keeping the details of motor skills away from forebrain computation, and (ii) signaling to the forebrain when a sensory event is *not* predictable from prior motor commands. However, it is unclear how current models of the cerebellum could carry out these roles. Their architecture, based on the seminal ideas of Marr and Albus, appears to need ‘motor error’ to learn correct motor commands. However, since motor error is the difference between the actual motor command and what the command should have been, it is a signal unavailable to the organism in principle. We propose a possible solution to this problem, termed decorrelation control, in which the cerebellum learns to decorrelate the motor command sent to the muscles from the *sensory consequences* of motor error. This method was tested in a linear model of oculomotor plant compensation in the vestibulo-ocular reflex. A copy of the eye-movement command was sent as mossy-fiber input to the flocculus, represented as a simple adaptive filter version of the Marr–Albus architecture. The sensory consequences of motor error were retinal slip, delivered as climbing fiber input to the flocculus. A standard anti-Hebbian learning rule was used to decorrelate the two. Simulations of the linearized problem showed the method to be effective and robust for plant compensation. Decorrelation control is thus a candidate algorithm for the basic cerebellar microcircuit, indicating how it could achieve motor learning using only signals available to the system. Such learning might then enable the cerebellum to free up visual awareness, and also, by providing a sensory signal decorrelated from motor command, supply awareness with crucial information about the external world.

## Introduction

Those of us fortunate enough to have worked with Alan Cowey in the laboratory are aware of both his practical skills and his helpfulness. But the example set by Alan extends beyond the laboratory. Anyone who has read his account of global stereopsis in rhesus monkeys (Cowey et al., 1975) will know about the cunning those animals use to seize on cues the experimenter did not intend them to employ. They will also be aware of this particular experimenter’s ability not to be taken in by plausible though attractive explanations of his subjects’ performance, to think of alternative although unwelcome explanations,

and to pursue the evidence needed to find the explanation that is correct. This approach in its combination of intellectual honesty and acuity has similarities to that immortalized in the great fictional detective, Sherlock Holmes, and is just as relevant to theoretical investigations of neural function as it is to experiments in the laboratory. And it is with theoretical studies, specifically with computer modeling of cerebellar function, that this present contribution deals.

## *The cerebellum and visual awareness*

A long-standing view of cerebellar function concerns its ability to free the forebrain from the detailed calculation required to generate accurate movement.

\*Corresponding author. Tel.: +44-(0)114-222-6521;  
Fax: +44-(0)114-276-6515; E-mail: p.dean@sheffield.ac.uk

49 An early formulation was by Brindley in 1964:

50

51 “the message sent down by the fore-brain  
52 in initiating a voluntary movement is often  
53 insufficient...it needs to be elaborated  
54 by the cerebellum in a manner that  
55 the cerebellum learns with practice... The  
56 cerebellum is thus a principal agent in the  
57 learning of motor skills.” (Brindley, 1964).

58

59 This idea has been particularly influential in  
60 guiding cerebellar modeling:

61

62 “...the cerebellum becomes rather more  
63 than a slave which copies things originally  
64 organized by the cerebrum: it becomes an  
65 organ in which the cerebrum can set up  
66 a sophisticated and interpretative buffer  
67 language between itself and muscle.  
68 This...leaves the cerebrum free to handle  
69 movements and situations in a symbolic  
70 way without having continually to make  
71 the translation.” (Marr, 1969) p. 468.

72

73 From this perspective, the cerebellum fulfils a  
74 role similar to that of a certain kind of computer  
75 operating system: easy-to-use high-level commands  
76 are translated into the requisite machine language.  
77 It is the cerebellum that makes the body user-friendly.

78

79 An intuitive mapping of this idea onto the field  
80 of awareness suggests that without a cerebellum,  
81 much of our conscious thought would be spent in  
82 making sure we did not fall over, in planning how  
83 to set one foot in front of another, and in working out  
84 how to move our eyes to look at the next target  
85 of interest in the visual scene. But since the cerebellum  
86 learns to execute such skills automatically, awareness  
87 is spared the necessary detailed planning, and is at  
88 liberty to focus on our internal representations of the  
89 visual world. In reading, for example, the cerebellum  
90 allows awareness of the meaning of the text to be  
91 unsullied by complex planning of the next saccade.

92

93 This is not, however, the only suggestion concern-  
94 ing the role of the cerebellum in awareness. A  
95 number of workers have been at pains to emphasize  
96 that the cerebellum is not only (or even primarily)  
involved in motor functions, but instead plays a  
role in the acquisition and analysis of sensory input

(Paulin, 1993; Bower, 1997). For example, the cerebellum may help to clarify whether a given stimulus results from the system’s own movements, or whether instead it is unexpected and hence of external origin (Blakemore et al., 2001; Nixon and Passingham, 2001). Thus, the cerebellum has been implicated in our inability to tickle ourselves (Weiskrantz et al., 1971; Blakemore et al., 2000). Again, mapping these notions loosely onto the field of awareness suggests that the cerebellum might act as a kind of gatekeeper which reduces the salience of stimuli that were in some sense to be expected.

### Problems with models of the cerebellum

A minimal requirement for the plausibility of these suggestions about cerebellar roles in awareness is that models of the cerebellum are capable of carrying out the necessary calculations. Unfortunately, it is far from clear that this is in fact the case. As a background to understanding the problems of cerebellar models, it is helpful to recall some very basic features of the anatomy and physiology of cerebellar cortex (Eccles et al., 1967; Kandel et al., 2000).

#### *Background to cerebellar models*

Cerebellar cortex has only one type of output cell, namely the Purkinje cell (schematic in Fig. 1), distinguished by its spectacular dendritic field. Purkinje cells receive two types of excitatory inputs, delivered by mossy fiber and climbing fiber afferents to cerebellar cortex. Mossy-fiber synapses contact granule cells, the most numerous neuronal cell type in the entire brain, whose axons ascend to the surface of the cortex then bifurcate to become parallel fibers. Both ascending axons and parallel fibers form excitatory synapses on Purkinje cells, which cause the cell to fire normal (termed ‘simple’) spikes at tonic rates of about 100 Hz. An individual Purkinje cell will receive input from many thousands of granule cells: in contrast, it is contacted by only one climbing fiber. However, this fiber wraps itself around the dendritic tree of the Purkinje cell, forming multiple synapses that ensure the Purkinje cell fires whenever the climbing fiber does. The ‘complex’

97 spike so produced is longer lasting than the usual  
 98 simple spikes, but occurs much less frequently  
 99 (about 1 Hz).

100 Since many current cerebellar models are in effect  
 101 descendants of the original models of Marr (1969)  
 102 and Albus (1971), they tend to explain the above  
 103 features of cerebellar cortex in similar ways (Fig. 2).

- (1) Decomposition of mossy-fiber inputs. The trans-  
 formation of mossy-fiber input into parallel fiber

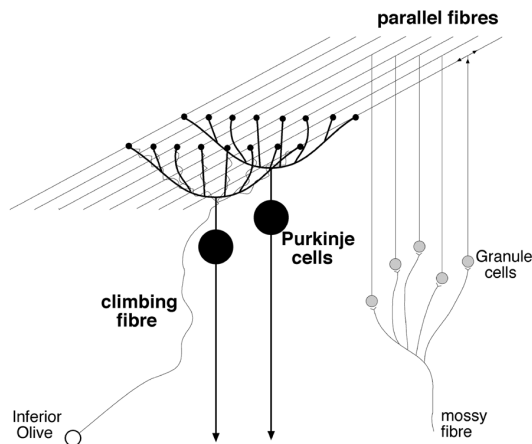


Fig. 1. Highly simplified sketch of the neural circuitry of cerebellar cortex, showing only the main excitatory inputs to Purkinje cells.

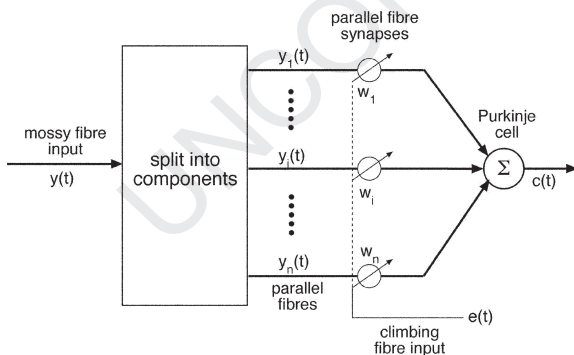


Fig. 2. Interpretation of simplified cerebellar circuitry in Marr-Albus framework. Mossy-fiber input  $y(t)$  is split into components  $y_i(t)$  that are conveyed by parallel fibers. Each component is weighted by  $w_i$  which corresponds to the efficacy of the synapse between that parallel fiber and the target Purkinje cell. The weighted components are summed to produce Purkinje cell output. The value of each weight can be altered by climbing-fiber input  $e(t)$ , which acts as a teaching signal.

activity is seen as splitting the input signal into simpler components. These simpler components make *learning* easier.

- (2) Recombination of parallel fiber signals. Synapses between parallel fibers and Purkinje cells are seen as ‘weighting’ signal components. The Purkinje cell *simple spike* output is generated from these weighted components.
- (3) Weights altered by climbing fiber signals. Climbing fiber input is seen as altering the values of these weights, i.e. the parallel-fiber Purkinje-cell synapses. Climbing fiber input acts as a *teaching signal*, enabling the cerebellum to be involved in motor learning. This idea can in principle explain both the power of the climbing fiber input (*all* parallel fiber synapses must be affected) and its relative weakness (very low frequency of complex spikes, so the output of Purkinje cell is scarcely affected).

### Shortcomings of cerebellar models

Why does this type of model have problems producing the kind of cerebellar behavior required for the interactions with visual awareness described above? As far as signaling unexpected sensory events is concerned, Marr-Albus-type models have tended to concentrate on the motor aspects of cerebellar function (cf. the quotation from Marr above). Possible sensory functions of the cerebellum have to some extent been neglected.

However, even within the motor domain, it is not clear whether the Marr-Albus type of model actually works. Marr expressed this problem in general terms:

“In my own case, the cerebellar study... disappointed me, because even if the theory was correct, it did not enlighten one about the motor system — it did not, for example, tell one how to go about programming a mechanical arm.” (Marr, 1982) p. 15.

More particularly, a grave disadvantage of some versions of these models is that they appear to require ‘motor error’ as teaching signal. This is a generic problem of supervised learning algorithms, employed,

145 for example, with multilayer artificial neural  
 146 networks. Supervision takes the form of telling the  
 147 net what the difference was between its output and  
 148 the correct output. In the case of motor commands,  
 149 this difference (between the actual motor command  
 150 and the correct command) is termed motor error.  
 151 Using motor error as the teaching signal conveyed by  
 152 climbing fibers allows Marr–Albus models to learn  
 153 correct motor commands.

154 Unfortunately, a motor-error signal does not exist  
 155 in practice, because the system cannot know in  
 156 advance what the correct motor commands should  
 157 be. Perhaps not surprisingly then, experimental  
 158 investigations of climbing fiber signals suggest that  
 159 they are often sensory (concerning, e.g. touch, pain)  
 160 rather than motor in nature (Simpson et al., 1996).  
 161 How can the model learn the correct commands with  
 162 only sensory information as a teaching signal?

### 165 Decorrelation control as a possible solution

166  
 167 Decorrelation control has been suggested as a  
 168 possible algorithm for the cerebellum to solve both  
 169 the sensory and the motor problems (Dean et al.,  
 170 2002). It replaces motor error as a climbing fiber  
 171 signal by ‘sensory error’, that is the *sensory*  
 172 *consequences* of an incorrect motor response. For  
 173 example, poor aim in tennis sends the ball in an  
 174 unintended direction: the difference between actual  
 175 and intended direction is a form of sensory error.  
 176 (Motor error would be the difference in command to  
 177 the arm muscles required to move the racquet in the  
 178 necessary manner for accuracy.) The crucial point  
 179 about sensory error is that, in sharp contrast to  
 180 motor error, it could be available to the system —  
 181 visually, in the tennis example. But how could  
 182 sensory error be used in learning?

183 By definition, sensory error is caused by motor  
 184 error. Values of the relevant sensory variable (e.g.  
 185 in the tennis case, direction taken by ball in relation  
 186 to intended direction) will therefore be correlated  
 187 with preceding motor commands, if those commands  
 188 are incorrect. If, however, the commands are correct,  
 189 there will be no correlation between the commands  
 190 and the sensory variable. In tennis, deviations  
 191 between intended and unintended ball flight might  
 192 be caused by sudden gusts of wind, but would in that

case be uncorrelated with motor commands. The  
 purpose of decorrelation control is therefore to  
 remove any correlations between motor command  
 and the variable that codes sensory error.

Decorrelation control thus requires that some  
 mossy-fiber inputs (Figs. 1 and 2) carry information  
 relating to the motor command, for example an  
 efference copy. It also requires climbing fibers to  
 carry information about the undesirable sensory  
 consequences of motor commands. Finally, it uses  
 the following as a learning rule:

- (i) If parallel-fiber firing is positively correlated  
 with climbing-fiber firing, reduce the weight of  
 the parallel-fiber synapse with the Purkinje cell  
 (LTD).
- (ii) If parallel-fiber firing is negatively correlated  
 with climbing-fiber firing, increase the weight  
 of the synapse (LTP).
- (iii) If parallel-fiber firing is uncorrelated with  
 climbing-fiber firing, do not change the  
 synapse.

Although this rule may appear complex, its basic  
 equation is simple.

$$\delta\omega_i = -\beta e(t)y_i(t) \quad (1)$$

The change ( $\delta w_i$ ) in the weight ( $w_i$ ) of the synapse  
 between the  $i$ th parallel fiber and the target Purkinje  
 cell is proportional (with learning-rate constant  $\beta$ ) to  
 the product of the sensory error  $e(t)$  (climbing-fiber  
 signal) and the signal in the  $i$ th parallel fiber  $y_i(t)$  (all  
 signals expressed as differences from their tonic  
 levels). The equation is based on Sejnowski’s (1977)  
 characterization of anti-Hebbian learning at the  
 parallel-fiber Purkinje-cell synapse as a covariance  
 learning rule. It can be seen that learning will stop  
 ( $\delta w_i = 0$ ) if the expected value of the product of the  
 climbing-fiber signal  $e(t)$  and the parallel-fiber signal  
 $y_i(t)$  becomes zero, that is when there is no correlation  
 between  $e(t)$  and  $y_i(t)$ . If the parallel-fiber input  
 represents a component of motor command, learning  
 will cease when that component is decorrelated from  
 sensory error.

If the decorrelation-control algorithm were to  
 work, the cerebellum would be able to learn correct  
 motor responses by using an available sensory signal  
 (consequences of motor error), not the unavailable

193 signal of motor error itself. After learning, the  
 194 sensory signal would be uncontaminated by the  
 195 system's own motor commands, and would therefore  
 196 signal 'unexpected' sensory events. The algorithm  
 197 would therefore fulfil both the putative roles of the  
 198 cerebellum in relation to awareness.

### 201 Testing decorrelation control

203 A model of a neural process needs to pass at least two  
 204 types of test:

- 205 (i) Can it carry out the required computation?
- 206 (ii) Is it consistent with experimental evidence?

208 There has been extensive debate concerning the  
 209 relation of Marr–Albus-type models to the detailed  
 210 anatomy and physiology of cerebellar cortex (for  
 211 reviews, see [Llinás and Welsh, 1993](#); [Ito, 2001](#)). The  
 212 approach taken here is to focus on the first test,  
 213 namely whether the decorrelation-control algorithm  
 214 has the required computational power. This approach  
 215 in effect asks the question *if* the basic Marr–Albus  
 216 ideas are a reasonable simplification of cerebellar  
 217 physiology, *then* would decorrelation control work.  
 218 As far as the second kind of test is concerned, enquiry  
 219 will be limited to the issue of whether the inputs to  
 220 cerebellar cortex that are required by decorrelation  
 221 control (see above) are observed experimentally.

222 The computational problem facing the decorrela-  
 223 tion-control algorithm is implicit in Eq. (1). Although  
 224 learning will in fact cease once motor command and  
 225 sensory error are decorrelated, the question is  
 226 whether this state of affairs could ever be reached in  
 227 practice. If in Eq. (1) the term  $e(t)$  were to refer to the  
 228 difference between actual and desired cerebellar  
 229 output (motor error), the learning rule would  
 230 (under certain restrictions) be guaranteed to find the  
 231 values of the weights  $w_i$  ([Fig. 2](#)) that gave the best  
 232 (least-squares) estimate of cerebellar output.  
 233 However, the term  $e(t)$  in Eq. (1) in fact refers to  
 234 sensory error, that is the *effects* of cerebellar output  
 235 after it has been altered by the mechanical properties  
 236 of the system under control (summarized by the term  
 237 'plant'). Cerebellar cortex does not receive the infor-  
 238 mation, namely motor error, required to guarantee  
 239 learning (details in [Dean et al., 2002](#)). The first test  
 240 for the decorrelation-control algorithm is thus

whether it is capable of dealing with the kind  
 of plant characteristics that have been observed  
 experimentally.

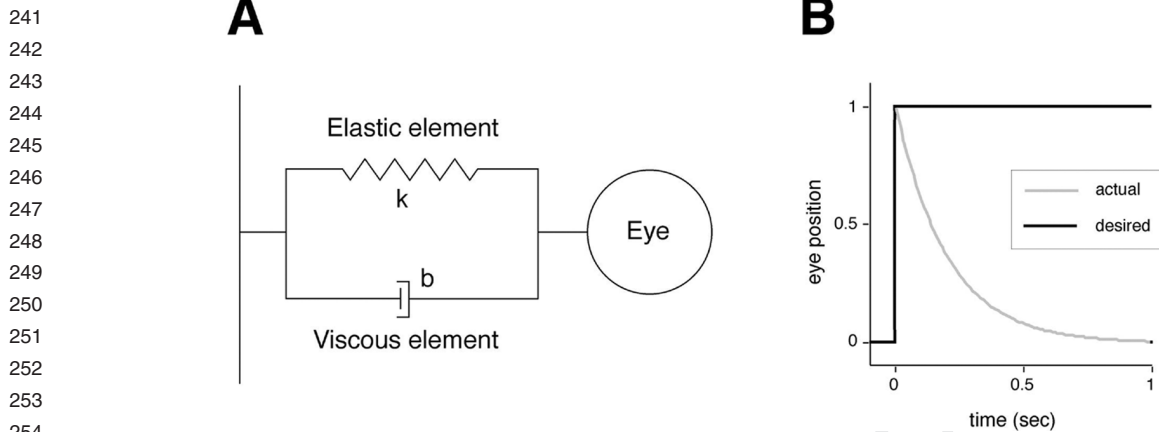
### *Oculomotor plant compensation*

We chose the oculomotor system to test decorrelation  
 control on the grounds that, compared with the  
 skeletal motor system, its mechanical properties are  
 relatively simple, and because a great deal is now  
 known about the anatomy and physiology of its  
 low-level control circuitry.

It appears that the inputs to this circuitry take the  
 form of eye-velocity commands. However, ocular  
 motoneuron output has to act on the eye muscles  
 and orbital tissue (the 'plant' referred to above).  
 The mechanical characteristics of the plant mean that  
 a simple velocity command does *not* generate the  
 corresponding velocity output ([Carpenter, 1988](#)).  
 This can be seen in [Fig. 3A](#) which illustrates a very  
 simple approximation to the oculomotor plant.  
 Although the inertia of the globe can be ignored for  
 most purposes, the plant still has elasticity as well as  
 viscosity, represented in [Fig. 3A](#) by a single elastic  
 element in parallel with the viscous element. This  
 elasticity distorts the velocity command, as shown in  
[Fig. 3B](#). Here a brief velocity command, similar to  
 that used to produce saccades, moves the eye rapidly  
 to a new position. But although the velocity  
 command after the brief pulse is zero, the eye  
 nonetheless moves, because the elastic element pulls  
 the eye back to the primary position. [Figure 3B](#)  
 shows the resultant exponential drift of eye position,  
 with time constant determined by the relative values  
 of the elasticity and viscosity. In the example  
 illustrated, the time constant is about 200 ms.

Prevention of this unwanted drift requires a  
 mechanism for producing the desired velocity output  
 (velocity in = velocity out). This mechanism is some-  
 times termed 'oculomotor plant compensation',  
 though in the oculomotor literature it is often  
 referred to as 'neural integration' since that is the  
 process required for a first-order plant as illustrated  
 in [Fig. 3B](#). Two important features of oculomotor  
 plant compensation qualify it as a suitable task for  
 testing the decorrelation-control algorithm.

First, there is good evidence that oculomotor plant  
 compensation requires the cerebellum. Lesions of the

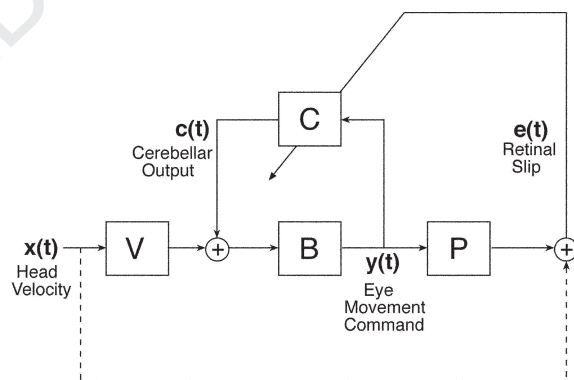


255 Fig. 3. (A) Simple model of oculomotor plant, consisting of an elastic element (with elasticity  $k$  with dimensions of force and distance<sup>-1</sup>) in parallel with a viscous element (viscosity  $b$  with dimensions of force and velocity<sup>-1</sup>). The inertia of the eyeball is ignored. 256 (B) Behavior of plant illustrated in A upon release from a position  $1^\circ$  from the resting position. The time course of the return to the 257 resting position is an exponential decay, with a single time constant given by  $b/k$  (in example shown here, = 0.2 s). 258

259 cerebellum that include a particular region produce 260 a postsaccadic drift back to the primary position 261 similar in appearance to that shown in Fig. 3B, 262 though with a longer time constant of about 1–2 s 263 (Carpenter, 1972; Robinson, 1974; Zee et al., 1981; 264 Godaux and Vanderkelen, 1984). (We use the term 265 flocculus for this region for simplicity, though the 266 adjacent ventral paraflocculus is also likely to be 267 involved). Secondly, the velocity in–velocity out rule 268 can be regarded as an example of the ‘elaboration’ 269 of an insufficient motor command, the generic 270 cerebellar function proposed by Brindley (1964) in 271 the quotation given above. 272

### 273 Structure of model

274 275 276 The process of learning oculomotor plant compensation 277 requires a source of velocity commands. A 278 suitable source is provided by the vestibulo-ocular 279 reflex (VOR), in which movements of the head send a 280 velocity signal through the brainstem to the eye 281 muscles. The goal of the reflex is to reproduce these 282 velocity commands (with appropriate sign) so that 283 the eyes counter-rotate to maintain stable gaze. If 284 this goal is not achieved, the eyes move relative to 285 the world, and so the whole image moves over the 286 retina, a movement known as ‘retinal slip’. Retinal 287 slip is the sensory error corresponding to the 288



273 Fig. 4. Simplified model for plant compensation in vestibulo-ocular reflex. Head velocity  $x(t)$  is processed by the filter  $V$ , then 274 added to the output  $c(t)$  of the decorrelator (cerebellar flocculus)  $C$ . The summed signal is then passed to a brainstem 275 controller  $B$ . The output of  $B$  is a motor command  $y(t)$ , which acts on the plant  $P$ . A copy of  $y(t)$  is sent back to the cerebellum 276  $C$ . The effects of  $y(t)$  acting on  $P$  are added to the head velocity  $x(t)$ ; the difference is detected as retinal slip  $e(t)$  and sent to  $C$ . If 277 there is no external visual signal acting on the eye, the desired 278 value of  $e(t)$  is zero. This will occur when the effects of the eye- 279 movement command  $y(t)$  acting on the plant  $P$  exactly match 280 those of the head velocity  $x(t)$  (from Dean et al., 2002). 281

282 motor error in eye-movement commands for gaze 283 stabilization.

284 The structure of the VOR model is shown in 285 Fig. 4, and a more detailed description is given in the 286 Appendix. The general problem of VOR control was 287

289 simplified in three ways. First, only the horizontal  
290 reflex was considered. Second, it was assumed that  
291 each component process within the model was  
292 linear. These components are the brainstem ( $B$ ), the  
293 cerebellum ( $C$ ), the oculomotor plant ( $P$ ), and a  
294 process ( $V$ ) for transforming head velocity into a  
295 neural signal. Third, it was assumed that  $V$  was  
296 veridical (i.e.  $V=1$ ).

297 The model of the cerebellar flocculus  $C$  received  
298 two inputs. One was a copy of the eye-movement  
299 command sent to the extraocular muscles, the other  
300 the retinal-slip signal. These are the inputs required  
301 by the decorrelation control algorithm, with the  
302 command copy as mossy-fiber input to be decorre-  
303 lated from sensory error as climbing fiber input. It  
304 is important to note the extensive anatomical and  
305 physiological evidence supporting the existence of  
306 these inputs (Lisberger and Fuchs, 1978; Miles et al.,  
307 1980; Stone and Lisberger, 1990; Büttner-Ennever  
308 and Horn, 1996; Simpson et al., 1996; Voogd et al.,  
309 1996). Moreover, experimental studies of oculomotor  
310 plant compensation in primate indicate that the  
311 process uses retinal slip, and depends upon the  
312 integrity of the flocculus (Optican and Miles, 1985;  
313 Optican et al., 1986).

314 The internal structure of the cerebellar flocculus  $C$   
315 was modeled as an adaptive linear filter (Widrow and  
316 Stearns, 1985), perhaps the simplest possible imple-  
317 mentation of the Marr–Albus ideas (Gilbert, 1974;  
318 Fujita, 1982). The structure of the adaptive linear  
319 filter is as shown in Fig. 2, with the constraints that  
320 the decomposition of mossy-fiber inputs into parallel-  
321 fiber signals, and the weighted recombination of  
322 those signals were both linear processes. In the  
323 version of the model described here, the components  
324 of the mossy-fiber signal were the original motor-  
325 command signal delayed by successive amounts  
326 (0.02 s between each component, 100 components).

327 The plant  $P$  was a first-order system with time  
328 constant = 0.2 s, as illustrated in Fig. 3. Although this  
329 is a simple approximation to the complexities of the  
330 real plant, it has nonetheless proved very useful in  
331 a range of modeling applications (Robinson, 1981).  
332 The brainstem  $B$ , intended to represent the medial  
333 vestibular nucleus and nucleus prepositus hypoglossi,  
334 had two components (details in Appendix). Their  
335 characteristics were intended to match those dis-  
336 played after lesions of the flocculus in primate

(Zee et al., 1981; Rambold et al., 2002). One was a  
direct pathway with a gain that accurately matched  
the head-velocity input to the eye-velocity output at  
high ( $>1$  Hz) frequencies. Thus, the basic gain of  
the VOR was not stored in the flocculus itself but  
in the brainstem (Luebke and Robinson, 1994;  
McElligott et al., 1998; Rambold et al., 2002). The  
second component was a leaky integrator with time  
constant 0.5 s, to be consistent with the observation  
that after cerebellar inactivation the time constant  
of postsaccadic drift is longer than that obtained for  
the plant alone (Carpenter, 1972; Robinson, 1974;  
Zee et al., 1981; Godaux and Vanderkelen, 1984).  
The performance of the brainstem controller is shown  
in Fig. 5. The retinal slip found in response to the  
training stimulus (head-velocity signals with a mix-  
ture of frequencies) shows good compensation at  
high frequencies (Fig. 5A), and indeed the gain of the  
system above about 1 Hz is close to one (Fig. 5B).  
After a velocity-pulse input, eye position relaxes back  
to the primary position with a time constant of  
about 1 s (Fig. 5C). Finally, because the brainstem  
controller is insufficient on its own to produce  
accurate motor commands, there are indeed correla-  
tions between components of the motor command  
and the subsequent sensory error, namely retinal slip  
(Fig. 5D).

## Results of decorrelation control

The effects of training the system just described with  
the decorrelation-control algorithm are shown in  
Fig. 6. Retinal slip declined rapidly at first, then more  
slowly (Fig. 6A), and was still continuing to decline at  
the end of 1000 trials of training (each trial = 5 s of  
colored noise head-velocity input). At this point the  
remaining slip was very slight (Fig. 6B), and the  
ability of the system to hold eccentric gaze after a  
velocity pulse was almost perfect (Fig. 6C). Finally,  
the correlations between motor-command compo-  
nents and sensory error had almost completely  
disappeared (Fig. 6D).

These findings demonstrate that the decorrelation-  
control algorithm is capable of learning accurate  
velocity commands, and thus compensating for  
the oculomotor plant, with the particular model-  
ing assumptions outlined in the section on model

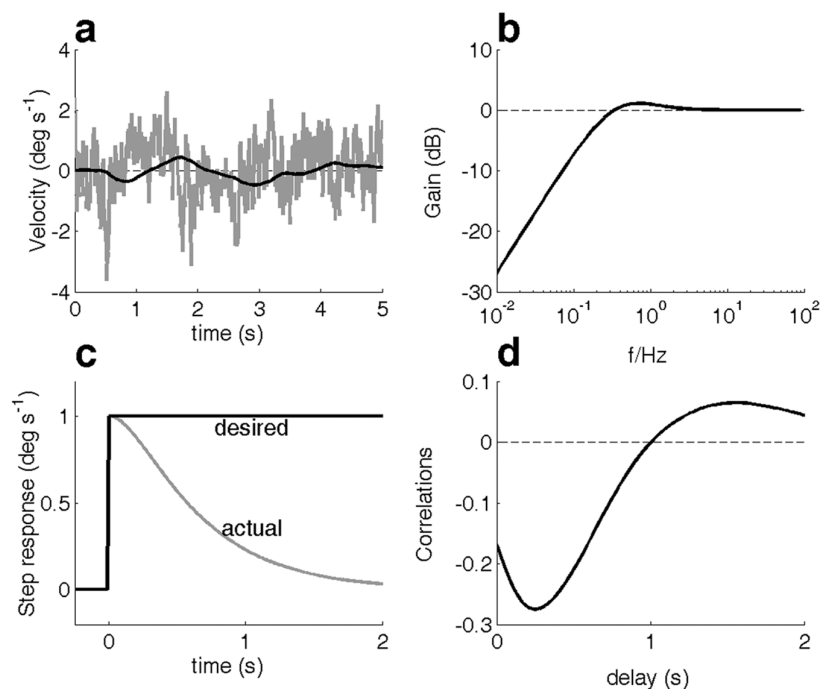


Fig. 5. Performance of the model before training, with a first-order plant  $P$  (time constant = 0.2 s). The brainstem controller  $B$  was a leaky integrator with time constant 0.5 s and accurate high-frequency gain. (A) Head velocity and retinal slip. The colored-noise head-velocity signal (root-mean-square amplitude 1°/s) produced a relatively smooth retinal slip signal. (B) The reason for the smoothing is evident from the Bode plot of VOR gain against frequency of head velocity. For frequencies above about 1 Hz the VOR gain is close to 1.0, because of the properties of the brainstem controller. (C) Eye-position response of system to a head-velocity pulse (equivalent to head-position step, and similar to a saccadic eye-movement command). The eye position returns to its initial value with a time course determined by the characteristics of both the plant and the brainstem controller. (D) The correlations present between delayed versions of the eye-movement command and retinal slip, measured over a period of 500 s (modified from Dean et al., 2002).

structure. The next test for the algorithm is whether it is robust, that is to say whether it can still cope when those assumptions are relaxed. The following assumptions were investigated.

- (i) There are still uncertainties about the precise characteristics of the brainstem controller  $B$  (De Zeeuw et al., 1995). We tested the extreme case of having no brainstem controller at all (i.e.  $B$  set to a gain of 1) Although learning was slow, eventual convergence was good and the asymptotic performance for both retinal slip and eccentric gaze resembled that shown in Fig. 6. Thus, the success of the decorrelation-control algorithm does not depend on the precise characteristics of the brainstem controller.
- (ii) The first-order plant used above is the simplest dynamical system possible. What happens

when decorrelation control is confronted with a more realistic model plant? We approached this question in two ways. First, we replaced the single-element plant of Fig. 3 with a two-element model (details in Appendix), of the kind suggested by behavioral and electrophysiological data (Optican and Miles, 1985; Optican et al., 1986; Fuchs et al., 1988; Stahl, 1992; Goldstein and Reinecke, 1994; Goldstein et al., 2000). This plant shows substantially more complex behavior and requires more sophisticated control, including a ‘slide’ of innervation after a velocity pulse (Optican and Miles, 1985; Goldstein and Reinecke, 1994; Goldstein et al., 2000). Nonetheless, the decorrelation-control algorithm was able to learn to compensate a two-element plant (Fig. 7, details in legend). Secondly, the learning



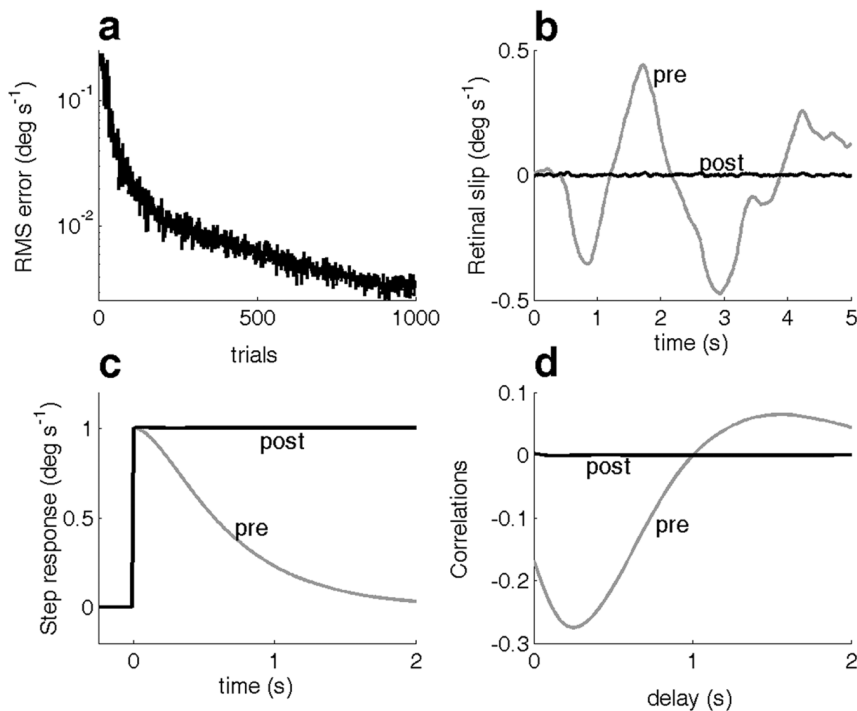


Fig. 6. Performance of model during and after training, with a first-order plant  $P$  (time constant = 0.2 s) and a brainstem controller  $B$  with a leaky integrator (time constant 0.5 s) and accurate high-frequency gain. (A) Typical decline in retinal-slip amplitude with training. Root-mean-square retinal-slip amplitude, measured over a 5-s training trial as shown in Fig. 4A, plotted on a log scale against number of training trials. (B) Posttraining reduction in retinal slip (note change in scale from Fig. 4A). (C) Eye-position response of system to a head-velocity pulse. The resultant eccentric eye position is maintained. (D) The pretraining correlations between delayed versions of the eye-movement command and retinal slip have almost disappeared (modified from Dean et al., 2002).

properties of the configuration shown in Fig. 4 were analyzed mathematically (Porrill et al., 2003). The analysis revealed that the synaptic weights become more accurate as long as output errors are being made. Thus, the algorithm is guaranteed to learn to compensate for any plant (subject to certain technical limitations). The crucial point is that the system operates in ‘feedback’ mode, i.e. a copy of the motor command is fed back to the cerebellum. This general result is important, not least for the specific case of oculomotor plant compensation where a variety of data suggest that the oculomotor plant may contain at least three viscoelastic elements (Robinson, 1965; Sklavos et al., 2002). The mathematical analysis indicates that the decorrelation-control algorithm is capable of compensating for these more complex plants.

- (iii) Concerns have been expressed about the capacity of the climbing-fiber pathway to convey detailed information because the maximum firing rate of an individual fiber is rather low, that is about 10 Hz. However, when the decorrelation-control algorithm was tested with a climbing-fiber signal that conveyed only the *direction* of retinal-slip (not its magnitude) learning was still similar to that illustrated in Fig. 6. The main difference was that final performance needed to be improved slightly by reducing the learning rate ( $\beta$  in Eq. 1) near to convergence.
- (iv) A further problem with the climbing-fiber pathway is that the retinal-slip signal it delivers to the flocculus is delayed by about 100 ms (Miles, 1991). Such a delay introduces instabilities into the learning process if the training data contain frequencies higher than about 2.5 Hz (see Appendix). These instabilities can be

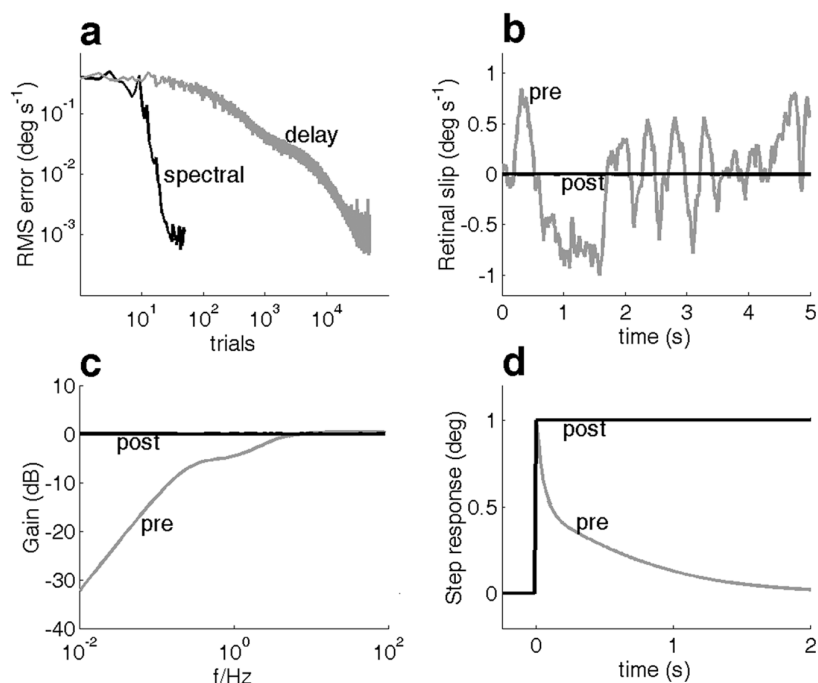


Fig. 7. The decorrelation-control algorithm used with a second-order plant  $P$  and a leaky-integrator brainstem controller  $B$ . (A) Learning as measured by reduction on root-mean-square retinal-slip amplitude. Note log scale on both axes. The two curves are for decorrelators with either the ‘delay’ or the ‘spectral’ set of basis functions. The latter were an orthogonal set derived from the principal components of compensated motor commands. The final performance of the trained filter was little affected by the basis functions used. (B) Pre- and posttraining retinal slip in response to a colored-noise head-velocity input. (C) Pre- and post-training Bode gains for the VOR. (D) Pre- and posttraining eye-position response to a head-velocity pulse (from Dean et al., 2002).

avoided by what has been termed an ‘eligibility trace’, which acts as a delay and smoothing filter to remove high frequencies from the motor-command components (details in Appendix). A variety of behavioral and electrophysiological evidence points to the existence of an eligibility trace (Raymond and Lisberger, 1998; Wang et al., 2000; Kehoe and White, 2002).

- (v) Finally, very little is known about the way mossy-fiber signals are decomposed into parallel-fiber components. Our use of different delays in the simulation described above is essentially an educated guess. However, by trying different schemes for decomposing signals in the adaptive linear filter, we were able to show that their main influence was on the speed with which the decorrelation-control algorithm learns, rather than its final convergence. Suitable choice of decomposition method could in fact speed learning very

considerably (Fig. 7). Suggestions that the method of decomposition can itself be influenced by learning (implemented for example by synaptic plasticity between mossy fiber–granule cell complex) have been made elsewhere (Schweighofer et al., 2001).

To summarize, the above results indicate that in the context of the flocculus and (linearized) oculomotor plant compensation, the decorrelation-control algorithm is an effective and robust method of ensuring that a simple velocity command into the system generates the corresponding velocity output.

### Decorrelation control and visual awareness

One of the roles suggested for the cerebellum in relation to awareness is that it carries out the ‘elaboration’ of simple motor commands issued by the forebrain, thereby freeing the forebrain’s computational

resources. But it seemed that in order to learn such elaboration, cerebellar models — at least those based on the ideas of Marr and Albus — required a signal that *in principle* could not be available, namely motor error. However, the decorrelation control algorithm is a possible solution to this problem, since it requires an available signal of the sensory consequences of motor error, not motor error itself. The results described above indicate that for eye movements decorrelation control used by a simplified Marr–Albus model was effective in learning to compensate for a linearized oculomotor plant, thus enabling higher centers to send only simple velocity commands downstream with consequent easing of their computational load.

The second role mentioned above for the cerebellum in visual awareness concerned the provision of sensory information uncontaminated by the organism’s own activity. In the case of oculomotor plant compensation the sensory signal is whole-field retinal image movement (retinal slip), potentially contaminated by inaccurate eye-movement commands. Inasmuch as decorrelation control successfully removes this contamination, any retinal slip

remaining is a genuine external signal. This can be seen in a redrawing of the VOR circuitry (Fig. 4) to emphasize its sensory-processing aspect (Fig. 8). In the redrawn version the retinal slip that would occur if the retina did not move can be considered as a sensory ‘target variable’. This has two components: an external signal of interest  $u$ , combined with self-produced interference  $n$ . What the system is trying to do is move the sensor surface (i.e. the eye) so as to cancel  $n$ , leaving behind the ‘real’ signal  $u$ . The eye movement can thus be regarded as an estimate of that interference  $\hat{n}$ , and the resultant retinal slip an estimate of the real signal  $\hat{u}$ . The more accurate the eye movement, the better the estimate  $\hat{u}$  (so that if  $u$  were zero, for example, there would be no retinal slip at all). Thus, the decorrelation-control algorithm that learns to produce accurate eye movements necessarily produces a good estimate of the signal of interest. Consequently, decorrelation control is a candidate algorithm for securing *both* of the proposed functions of the cerebellum in visual awareness.

Of course, many questions remain. One of the most important concerns movements of parts of the

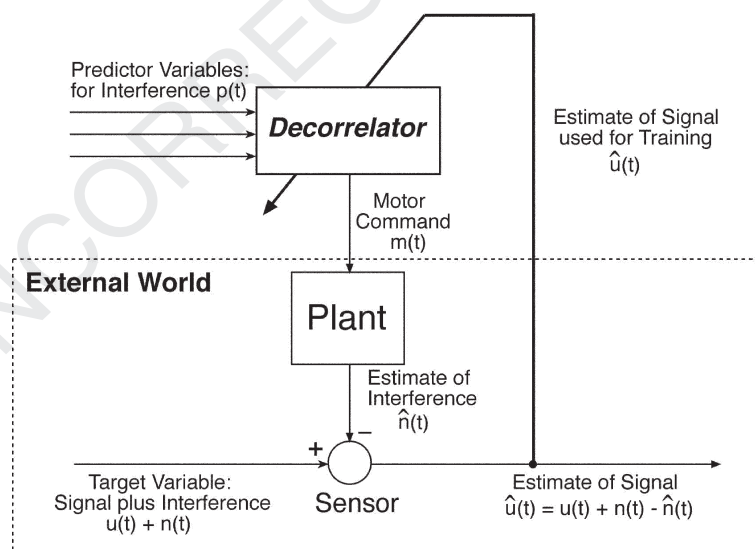


Fig. 8. Redrawing of the vestibulo-ocular circuitry shown in Fig. 4 to emphasize its sensory-processing aspects. Inputs to the system are: (i) the retinal slip that would occur if the eyes remain stationary is treated as a target variable. As such it consists of an external signal of interest  $u(t)$  corrupted by additive interference  $n(t)$ ; and (ii) predictor variables  $p(t)$ . The task of the system is to extract an estimate of the signal of interest  $\hat{u}(t)$  from the target variable. It does so by subtracting from the target variable an estimate  $\hat{n}(t)$  of the interference, in this case by physically moving the eye. Sensor output is no longer the target variable  $u(t) + n(t)$  but the estimate  $\hat{u}(t)$  of the signal of interest  $u(t)$ . The decorrelator must therefore learn the motor command  $m(t)$  which will act on the plant to produce the appropriate interference estimate (from Dean et al., 2002).

529 body other than the eyes. Unfortunately, control of  
 530 multijoint movements is more complex than eye-  
 531 movement control, and less is known about the  
 532 anatomical details of the projections of cerebellar  
 533 microzones to and from the relevant premotor  
 534 circuitry in cortex, brainstem, and spinal cord.  
 535 However, the mathematical analysis of decorrelation  
 536 control indicated that it was in principle capable of  
 537 compensating for very complex plants provided a  
 538 copy of the motor command was made available to  
 539 the relevant region of the cerebellum. It is therefore  
 540 interesting that Eccles (1973) supposed this to be the  
 541 case for motor cortex itself (the basis of his ‘dynamic  
 542 loop’ hypothesis). More recently anatomical investi-  
 543 gations using transneuronal transport methods have  
 544 indicated that a given area of cerebral cortex which  
 545 projects to cerebellar cortex via the pons receives  
 546 a projection back from that selfsame region of  
 547 cerebellar cortex via the thalamus. These “closed-  
 548 loop circuits may be a fundamental feature of  
 549 cerebellar interactions with the cerebellar cortex”  
 550 (Middleton and Strick, 2000, p. 240). It is possible  
 551 therefore that the closed-loop arrangements required  
 552 by decorrelation control are characteristic not just of  
 553 eye movements but of movements in general.

554 Further investigation of cerebro-cerebellar con-  
 555 nectivity is but one example of the extensive work  
 556 required to establish decorrelation control (or any  
 557 other candidate) as the generic cerebellar method. It is  
 558 of course a form of detective work, the kind of work  
 559 of which, as this volume attests, Alan Cowey is a  
 560 master.

## 562 Appendix

563  
 564 The model architecture of Fig. 4 was programmed in  
 565 MATLAB<sup>TM</sup>.  $P$ ,  $V$ ,  $B$ , and  $C$  were treated as linear  
 566 processes, allowing use of functions in the control  
 567 system toolbox. The characteristics of the linear  
 568 processes in initial training were:

- 569 (i)  $V$  was a unit gain.  
 570 (ii)  $P$  was a first-order plant, with the transfer  
 571 function  $H_p(s)$  between eye-in-head velocity  $e_h$   
 572 and motor command  $y$  given by Eq. (A1).  
 573

$$574 \quad H_p(s) = \frac{e_h(s)}{y(s)} = \frac{s}{s + 1/T_p} \quad (A1)$$

575  
 576

- where  $s$  denotes the Laplace complex fre-  
 quency variable and  $T_p$  the time constant of  
 the plant ( $=0.2$  s). (In subsequent equations  
 with transfer functions, the argument ( $s$ ) of  
 transfer functions is omitted for simplicity.)  
 (iii) The brainstem  $B$  had the transfer function  $H_b$   
 given by:

$$H_b = G_d + \frac{G_i}{s + 1/T_i} \quad (A2)$$

- corresponding to a brainstem controller with  
 two paths: (a) a direct path which passed the  
 head-velocity signal to the plant with the  
 correct gain ( $G_d = 1$ ); and (b) an indirect path  
 in which the head-velocity signal was integrated  
 and passed to the plant also with the correct  
 gain ( $G_i = 1/T_p = 5$ ). The brainstem integrator  
 was leaky with time constant  $T_i = 0.5$  s.  
 (iv) The input to the adaptive filter  $C$  was split into  
 100 components with delays between compo-  
 nents of 0.02 s (2 s total).  $C$  was thus effectively  
 a finite impulse-response filter of length 100,  
 with output  $c(t)$  given by:

$$c(t) = \sum_{i=1}^{100} w_i y_i(t - 0.02i) \quad (A3)$$

where  $w_i$  was the weight of component  $y_i$ . The  
 rule for adjusting the weights was equivalent to  
 that given in Eq. (1) in the text. The value of  
 the learning-rate constant  $\beta$  in that equation  
 was adjusted to give rapid learning without  
 instability.

The training input to the system was a head-  
 velocity signal modeled as colored noise with unit  
 power. The power had its peak value at 0.2 Hz, then  
 varied with increasing frequency  $f$  as  $1/f$  (as would  
 occur if white-noise head acceleration were integrated  
 to head velocity). For efficiency weight update was  
 implemented in batch mode using 5 s batches of  
 head-velocity data.

After training with the basic system described  
 above, a number of variants were investigated.

- (i) *Variants of B*: The integrator pathway was  
 removed (Eq. A2, with  $G_i = 0$ ).

- (ii) *Variants of P*: A second-order version of  $P$  was used with transfer function  $H_p$  given by:

$$H_p = \frac{s(s + 1/T_z)}{(s + 1/T_1)(s + 1/T_2)} \quad (\text{A4})$$

where  $T_1 = 0.37$  s,  $T_2 = 0.057$  s,  $T_z = 0.2$  s, taken from Stahl's estimate (Stahl, 1992, p. 361) of the best-fit two-pole one-zero transfer function (for eye position from eye-movement command) to the data of Fuchs et al. (1988). This plant was combined with a leaky undergained integrator (Eq. A2, with  $G_i = 5.05$ ,  $T_i = 0.5$ ).

- (iii) *Learning rule*: The learning rule was changed from that shown in Eq. (1) to:

$$\delta w_i = -\beta \text{sign}[e(t)]y_i(t) \quad (\text{A6})$$

and used to train an adaptive filter  $C$  with a first-order plant (Eq. A1) and a leaky undergained brainstem controller (Eq. A2,  $G_i = 2.5$ ,  $T_i = 0.5$ ).

- (iv) *Delay*: The retinal-slip signal arriving at  $C$  was delayed by  $d = 100$  ms. The system was trained with a first-order plant (Eq. A1) and a leaky undergained brainstem controller (Eq. A2, with  $G_i = 2.5$ ,  $T_i = 0.5$ ). It was found that the delay caused unstable learning if the input to  $C$  contained frequencies above  $1/4d$  (at these frequencies the input becomes  $> 90^\circ$  out of phase with the retinal-slip signal). The components  $y_i(t)$  were therefore convolved with an 'eligibility trace'  $r(t)$ . The equation for the eligibility trace was taken from Eqs. (11) and (12) of Kettner et al. (1997):

$$r(t) \propto t e^{-(t/t_{\text{peak}})} \quad (\text{A5})$$

where  $t_{\text{peak}}$  was set to 0.1 s.

- (v) *Basis functions*: The different delays used as basis functions for the mossy-fiber input  $y(t)$  were subsequently replaced by alternative functions. These included sine waves of different frequencies and decaying exponentials of different time constants, as well as basis functions that were orthogonalized with respect to the motor commands themselves. One method of achieving this was by spectral decomposition, in which the

motor outputs for a perfectly compensated first-order plant were subjected to principal component analysis. The 100 eigenvectors derived from the analysis were then used as basis functions. Learning was examined for the second-order plant with leaky undergained brainstem controller (variant 2 above).

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