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Recurrent cerebellar architecture solves the motor-error problem

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Current views of cerebellar function have been heavily influenced by the models of Marr and Albus, who suggested that the climbing fibre input to the cerebellum acts as a teaching signal for motor learning. It is commonly assumed that this teaching signal must be motor error (the difference between actual and correct motor command), but this approach requires complex neural structures to estimate unobservable motor error from its observed sensory consequences. We have proposed elsewhere a recurrent decorrelation control architecture in which Marr–Albus models learn without requiring motor error. Here, we prove convergence for this architecture and demonstrate important advantages for the modular control of systems with multiple degrees of freedom. These results are illustrated by modelling adaptive plant compensation for the three-dimensional vestibular ocular reflex. This provides a functional role for recurrent cerebellar connectivity, which may be a generic anatomical feature of projections between regions of cerebral and cerebellar cortex.

Keywords: cerebellum; motor control; vestibular

1. INTRODUCTION

Investigations of the structure and plasticity of the cerebellar cortex have revealed a basic cerebellar microcircuit (Ito 1984), which is repeated throughout the cerebellar cortex, in which information about the current sensory and motor state of the organism is obtained from the mossy fibre inputs to the cerebellum and distributed across the parallel fibre (PF) inputs to Purkinje cells (PCs) (see figure 1*a*). PCs also receive an input from a single climbing fibre (CF) and in Marr–Albus models (Marr 1969; Albus 1971) this input can alter the efficacy of PF–PC synapses. This microcircuit has been interpreted as an adaptive filter (see figure 1*b*; Gilbert 1974; Fujita 1982), which can be used to correct or fine-tune future motor behaviour based on current errors in performance. One of its major roles is thought to be the translation of 'simple' motor commands into the detailed instructions required for accurate movements (Brindley 1964; Marr 1969), a task that entails the adaptive compensation of the time-varying biological motor plant (muscles, tendons, linkages, etc.). However, the neural architecture required for an adaptive filter to perform plant compensation has proved difficult to identify.

Feedback error learning is the most complete current model of the role of the cerebellar microcircuit in plant compensation. It is based on the architecture shown in figure 2*a*, which corresponds to fig. 2*a* of Kawato (1990) and fig. 1*b* of Wolpert *et al.* (1998), and its properties can be derived informally as follows. The cerebellar filter C can be regarded as a single-layer neural net with adjustable weights, hence the training signal required for gradient descent learning is the error $\tilde{e}(t)$ in the output of C. This is the difference between the actual and desired motor commands and is commonly called the motor error. However, the motor-error signal is not directly observable because the output of C passes through the motor plant

P before producing its sensory consequences. Only the sensory effects of motor error, which we will term sensory error $e(t)$, are directly observable. However, sensory error would not be a satisfactory training signal for the same reason that the error at the output units of a multilayer artificial neural net is not a suitable training signal for units in the middle layers (the so-called 'distal-error problem'). To solve this problem the feedback-error-learning architecture 'back-propagates' sensory error through the motor plant to recover an estimate of the unobservable motor error. This back-propagation step is achieved by hypothesizing neural 'reference structures' that approximate the inverse motor plant. These structures are shown as P_{approx}^{-1} in figure 2*a*.

This approach has two major defects. First, the reference structures required for stable learning are of similar complexity to the structures to be learned. Second, a motor-error teaching signal seems incompatible with current evidence suggesting a strong sensory component to CF discharge. Consequently, we refer to the need for a motor-error signal on the CFs as 'the motor-error problem'.

Our solution to the motor-error problem is based on the recurrent architecture shown in figure 2*b*. This architecture, which is consistent with anatomical and neurophysiological evidence (Optican *et al.* 1986; Büttner-Ennever *et al.* 1996; Voogd *et al.* 1996; Belton & McCrea 2000) (see § 3*a* for more details), has previously been shown in simulations to be capable of solving the one-dimensional vestibular ocular reflex (VOR) plant compensation problem (Dean *et al.* 2002). Here, we prove convergence for the architecture in a very general setting and demonstrate its important advantages for the modular control of systems with multiple degrees of freedom.

2. PROPERTIES OF THE RECURRENT ARCHITECTURE

Convergence can be demonstrated informally by the following graphical argument. Start at the centre of the flow diagram in figure 2*b* and regard $y(t)$ as the 'input' signal;
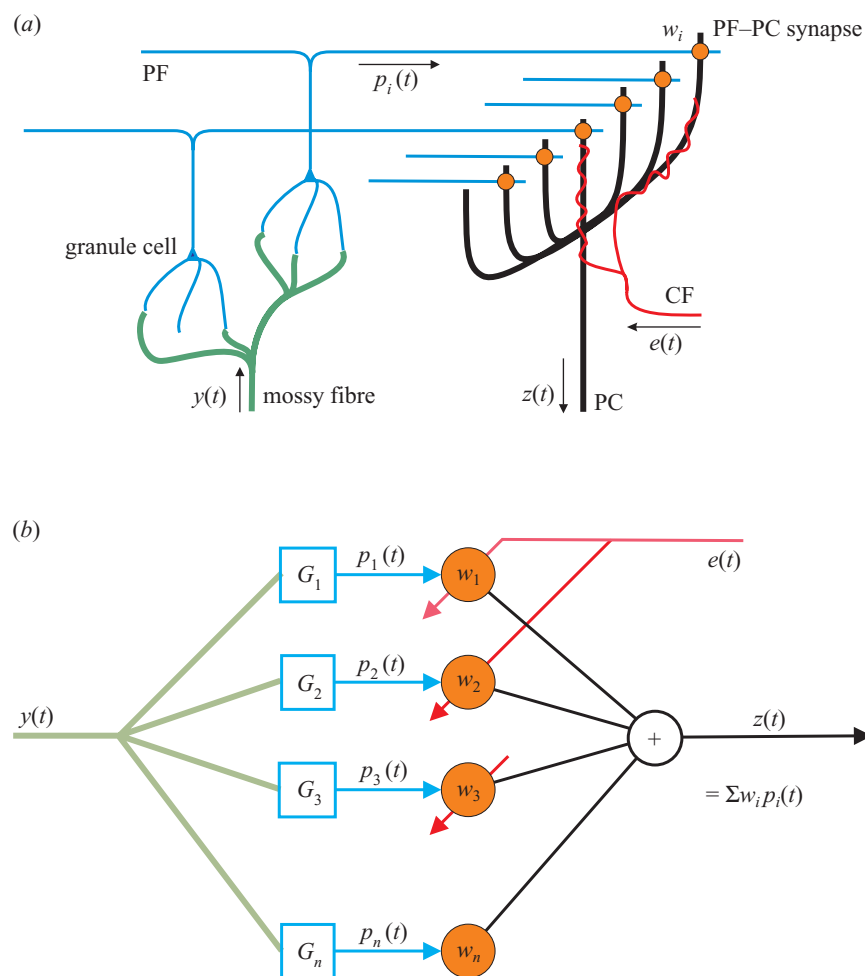
Figure 1. Schematic diagram of the organization of the cerebellar microcircuit and its interpretation as an adaptable linear filter (Fujita 1982; Kawato 1995). (*a*) A mossy-fibre input signal is distributed over many granule cells whose axons form PFs that synapse on PCs. In models of the Marr–Albus type correlated firing of a PF and the single CF that winds around the PC alters the efficiencies of the PF–PC synapses. In decorrelation control, mossy-fibre inputs are predictor variables, to be decorrelated from the target variable specified by the CF signal (Brindley 1964; Dean *et al.* 2002). (*b*) Processing of the MF input $y(t)$ by the granule cell layer is interpreted as analysis by a bank of linear filters G_i so that the PFs carry signals $p_i(t) = G_i * y(t)$. PC output is modelled as the weighted sum $z(t) = \Sigma w_i p_i(t)$ of these PF inputs, so the PC implements a linear filter $C = \Sigma w_i G_i$. The CF input is interpreted as a training signal $e(t)$, which adapts synaptic weights w_i using the hetero-synaptic covariance learning rule (Sejnowski 1977) $\delta w_i = -\beta \langle (p_i - \bar{p}_i)(e - \bar{e}) \rangle$. We will use this learning rule in the continuous-update form $\dot{w}_i = -\beta e p_i$ (where β is a small positive learning rate and all signals are taken as differences from their tonic levels). Note: the bank of filters G_i must be sufficiently rich to represent all C of interest but their exact nature is not critical.

going from left to right $y(t)$ passes through the filter P to give $\hat{x} = Py$, while going from right to left $y(t)$ passes through the filter $B^{-1} - C$ to give $x = (B^{-1} - C)y$ (this can be derived algebraically by solving the recurrent loop equation $y = B(x + Cy)$ for x). Looked at from this point of view, the error $e(t) = \hat{x} - x = (P - B^{-1} + C)y$ is measured at the *output* layer of the linear network C and so might be expected to form a suitable teaching signal without the need to back-propagate the error through any intermediate layers. The Lyapounov analysis presented in Appendix A confirms this heuristic reasoning, guaranteeing that synaptic weights become more accurate as long as output errors are made.

We now show that the two architectures we have described have very different implications for modularity in systems with many degrees of freedom (where the signals are vector valued). In the feedback error model a PC contributing to the ith component of motor output requires the ith component of motor error $\tilde{e}_i = \Sigma_j P_{ij}^{-1} e_j$ as a teaching signal. The connectivity between the sensory system and the cerebellum is thus specified by a tensorial structure P_{ij}^{-1}, dependent on the motor plant, whose complexity grows with that of the motor-command representation $y(t)$. By contrast, in the recurrent model a PC contributing to the ith component of input x_i simply receives CF information about the ith component of error e_i. The connectivity required here is entirely independent of the motor plant and of the motor-command representation.

Figure 3 illustrates this crucial difference in modularity between the two architectures using three-dimensional (3D) VOR plant compensation as a concrete example of an adaptable motor task with many degrees of freedom. In the schematic model shown, the three components of head angular velocity obtained from the vestibular system are processed by the brainstem and cerebellum to produce motor commands to the six extraocular muscles; this will counter-rotate the eye so as to stabilize the visual image against head movements.
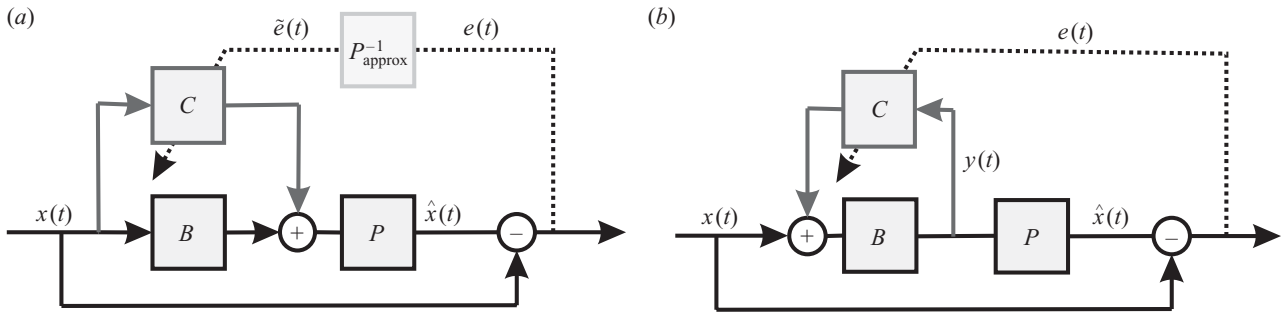
Figure 2. Alternative architectures for the cerebellar contribution to motor plant compensation. Task-space commands $x(t)$ must be converted into motor commands that will drive the plant P so as to set output error $e(t) = \hat{x}(t) - x(t)$ to zero. (a) Feedback-error-learning architecture: $x(t)$ is processed by a fixed element B (representing the brainstem in the case of the VOR) and by an adaptive element C (representing the cerebellum and implemented as in figure 1b). Their combined output drives the motor plant. Output error $e(t) = \hat{x}(t) - x(t)$ is processed by the approximate inverse plant P_{approx}^{-1} (highlighted by a light-grey box) to give a motor-error signal $\tilde{e}(t)$ suitable for training C. In the full model $\tilde{e}(t)$ is also used in a conventional feedback loop to drive the plant P. This path is omitted here for clarity. (b) Recurrent architecture. This differs from (a) in the direction of the cerebellar arcs (highlighted by dark-grey lines and box). The cerebellum now receives copies of the motor command $y(t)$ as its input, and its output is added to the input signal $x(t)$. We show that output error $e(t)$ is a suitable training signal in this architecture. It should be noted that this simplified diagram is not intended to suggest that: (i) $y(t)$ necessarily comes from the same brainstem cells that receive projections from the cerebellar cortex (see § 3a); or (ii) the flocculus lacks a vestibular input. The vestibular input is not included in this diagram because decorrelation control does not need it to compensate for the plant.
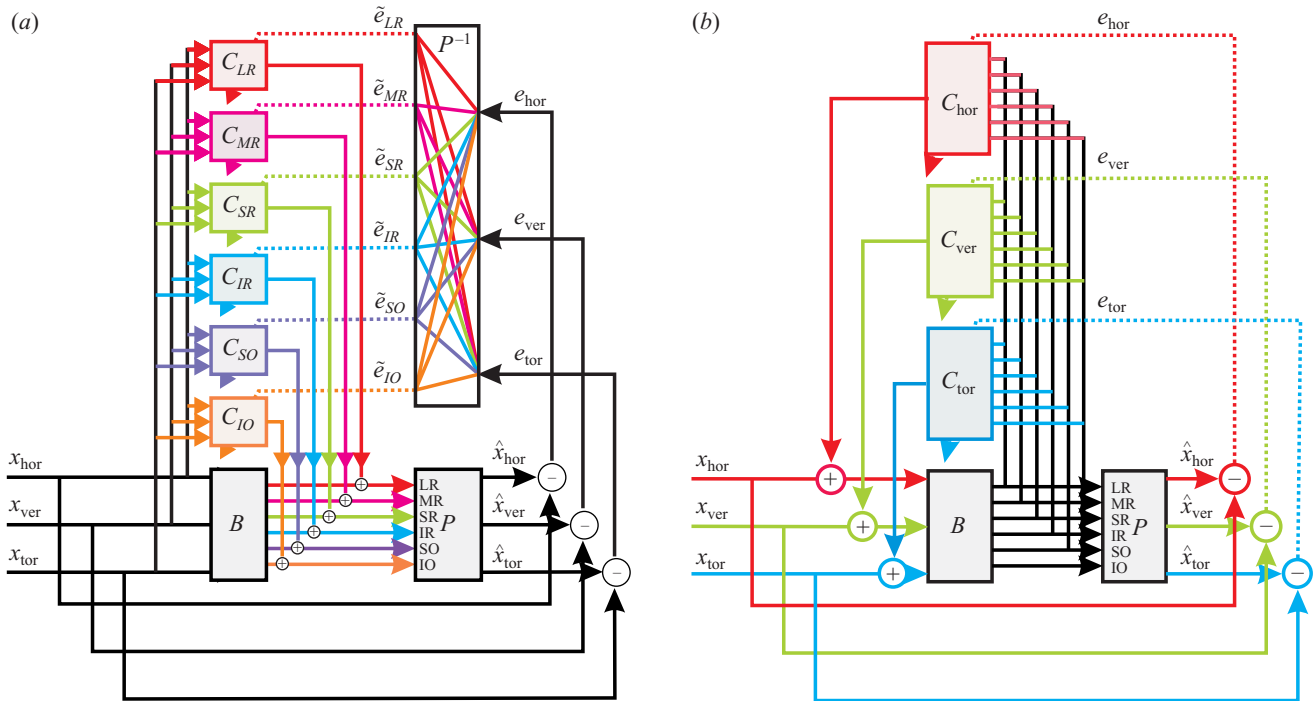

Figure 3. Alternative architectures applied to 3D VOR. The vestibular system recovers three components x_{hor}, x_{ver} and x_{tor} (horizontal, vertical and torsional) of head angular velocity. These are processed by the brainstem and cerebellum to produce motor commands to the six extraocular muscles so as to stabilize the eyes' rotational position in space. The motor plant is a 3×6 matrix transfer function P and the brainstem contribution to the VOR is a 6×3 matrix transfer function B. (a) Feedback-error-learning architecture: the cerebellum takes the three vestibular signals as input and supplies corrections to the six motor commands. Colour is used to highlight the 'motor space' modularity. For example the green component shows those PCs that contribute to the superior rectus (SR) muscle command, and which require the corresponding motor-command error $\tilde{e}_{\text{SR}}$ as a training signal on their CFs. This signal must be reconstituted from the horizontal, vertical and torsional components of retinal slip. (b) Recurrent architecture: the cerebellum takes the six motor commands as input and supplies corrections to the three vestibular signals. Colour is used here to highlight the 'task space' modularity. For example the green component shows PCs contributing to vertical eye motion; these require the vertical component of optic flow as a training signal.

Figure 3*a* shows the 'motor space' modularity induced by the feedback error architecture. Complex processing is needed to transform retinal-slip signals into motor errors for individual muscles. By contrast the recurrent architecture has the 'task space' modularity shown in figure 3*b*. Here (i) the simulated cerebellar flocculus receives copies of the motor commands to the six extraocular muscles as input (Büttner-Ennever *et al.* 1996; Belton & McCrea 2000); (ii) it is organized into three independent modules supplying corrections to the three components of head velocity obtained from the vestibular system (Voogd *et al.* 1996); and (iii) the teaching signal for a PC contributing to a given component of head velocity is simply the corresponding component of retinal slip (Graf *et al.* 1988) (it can be shown that this correspondence need only be approximate). The organization of the simulated flocculus shown in figure 3*b* is close to that indicated by neuroanatomical and neurophysiological evidence (e.g. Voogd *et al.* 1996).

Figure 4 shows the results of a computer simulation of 3D VOR plant compensation using the recurrent architecture illustrated in figure 3*b*. The initial state corresponds to the absence of any cerebellar contribution to VOR. It can be seen that during training all three components of retinal slip are reduced to zero at the rate predicted by theory and that after training there is accurate compensation for step changes in head position.

3. DISCUSSION

We have previously proposed decorrelation control as a candidate algorithm for the cerebellar microcircuit, in which cerebellar plasticity acts to reduce the correlations between predictor variables (mossy fibre signals) and a target variable (CF signals) (Dean *et al.* 2002). Our simulations indicated that the algorithm was effective and robust for oculomotor plant compensation in one dimension, with retinal slip used as a training signal and a copy of the eye-movement command as a predictor variable (i.e. a recurrent architecture). Here, we have extended that finding in two important ways: first by proving the efficacy of the proposed recurrent architecture for the general motor plant compensation problem; and second by showing that the use of sensory error instead of motor error as a training signal leads to a simpler and more plausible modular architecture for problems with multiple degrees of freedom, such as 3D oculomotor plant compensation.

We now discuss the following aspects of our proposed algorithm: the evidence for recurrent architecture in the particular problem of oculomotor plant compensation; the relationship of our algorithm to previous models of the cerebellum; predictions made by the model; and the general role of recurrent cerebellar connectivity.

(a) *Recurrent connectivity via the flocculus*

The wealth of neurophysiological information about the oculomotor system and its relative simplicity make it the natural test-bed for cerebellar modelling. The main cerebellar region concerned with oculomotor plant compensation has been identified as the flocculus (Zee *et al.* 1981; Optican *et al.* 1986; Graf *et al.* 1988; Voogd *et al.* 1996). It is well established that the flocculus receives visual and vestibular information (Noda *et al.* 1987; Markert

et al. 1988; Nagao 1990; Stone & Lisberger 1990). However, it is clearly crucial to the proposed model that the floccular region does in fact receive a substantial mossy-fibre input related to eye movement. The experimental evidence appears conclusive on this point.

Most directly, extensive electrophysiological recording of mossy fibres or other granular-layer input elements ($n = 771$) in the floccular regions of rhesus monkeys has indicated that 53.6% of the elements modulated their discharge solely in relation to eye movements (Miles *et al.* 1980). A further 21.7% showed eye-movement-related firing in addition to firing influenced by vestibular input. Thus, in total, 75.3% of floccular mossy-fibre-related inputs carry a signal related to eye movements. Other electrophysiological investigations of floccular mossy-fibre signals have reached similar conclusions (Lisberger & Fuchs 1978; Noda & Suzuki 1979), and it has been asserted that 'these oculomotor-related signals are generally assumed to represent some kind of efference copy signal' (Miles 1991, p. 225).

Additional evidence comes from anatomical studies (reviewed by Voogd *et al.* 1996) indicating that much of the mossy-fibre input to the flocculus comes from brainstem nuclei associated with eye movements, for example the medial vestibular nucleus, the nucleus prepositus hypoglossi, the abducens nucleus itself and the cell groups of the paramedian tracts (PMT). The last in particular have been proposed as candidates for providing a motor-feedback signal of extraocular-muscle activity to the floccular region (Dean *et al.* 2002). The properties of PMT cells in the cat are consistent with this proposal. Thus, electrophysiological recordings indicate that PMT neurons specifically identified as projecting to the flocculus carry signals relating to eye movements (Nakao *et al.* 1980; Cheron *et al.* 1996; Escudero *et al.* 1996). Moreover, inactivation of a subgroup of PMT cells that carry vertical eye-movement signals produces a gaze-holding impairment, consistent with a role in providing efference copy for plant compensation (Nakamagoe *et al.* 2000).

In summary, the results of a variety of experimental approaches support the view that the flocculus receives a mossy-fibre signal related to the eye-movement command, and the integrity of both the flocculus and this floccular input signal is necessary for oculomotor plant compensation.

(b) *Relationship to previous models of the cerebellum*

Comparison with previous cerebellar-modelling studies is not straightforward, because in many cases their aims were different from those of the present study. Our intention was to solve a fundamental computational difficulty with Marr–Albus architectures, namely their apparent requirement for physically unobtainable information about the desired motor output. From this perspective it was an advantage to use what is perhaps the simplest implementation of the basic Marr–Albus cerebellar microcircuit (Fujita 1982) to solve the generic motor problem of plant compensation. Other studies have tended to use more complex models, with the disadvantage that the added complexity makes theoretical comparisons of convergence and stability very difficult. The range of applicability of such models is also in doubt because

they have generally been applied to problems other than plant compensation and have often focused on specific rather than generic solutions (e.g. Kettner *et al.* 1997; Barto *et al.* 1999; Spoelstra *et al.* 2000; Assad 2001; Eskiizmirliler *et al.* 2002; Yamamoto *et al.* 2002). This applies even to models that have specifically used feedback via efference copy signals (Quaia *et al.* 1999; Hirata & Highstein 2001).

As far as we are aware, there is only one other model architecture that has been specified well enough to allow a detailed comparison of performance. This is the feedback error model described in § 1. The power of this architecture has been demonstrated by a number of simulations and by formal proofs of convergence. However, there appear to be two major problems with the feedback error architecture.

First is the requirement for complex 'reference structures' to recover a motor-error signal from the available sensory information, as seen in the example of 3D plant compensation (figure 3*a*). In the particular case of oculomotor plant compensation in the 3D VOR, the resultant connectivity and organization of the cerebellar flocculus are at odds with experimental evidence (Voogd *et al.* 1996). By contrast, the connectivity required by decorrelation control (figure 3*b*) is consistent with that evidence. For plant compensation in general, feedback error learning requires an already existing approximation to the inverse plant model it is trying to learn, so that 'the most interesting and challenging theoretical problem is setting an appropriate inverse reference model in the feedback controller at the spinal and brainstem levels' (Gomi & Kawato 1992, p. 112). The algorithm proposed here does not require a prior inverse plant approximation.

The second problem concerns the nature of the putative error signal conveyed by CFs. Feedback error learning requires this signal to approximate motor error—that is, the difference between actual and desired motor command. However, experimental evidence indicates that CFs are primarily activated by sensory inputs, such as touch, pain, muscle sense or, in the case of the VOR, retinal slip (Simpson *et al.* 1996; De Zeeuw *et al.* 1998). Insofar as these sensory inputs are modulated by movement-related signals (Gibson *et al.* 2002) or by the cerebellar output itself (Andersson *et al.* 1988), the resultant CF discharge appears to be related to the unpredicted sensory consequences of a movement, which is much closer to 'sensory error' as used here than to motor error as defined in § 1. Because errors in problems specified in task space can always be assessed by comparing sensory expectations with sensory reality, these findings support the simple assumption that the CF signal for motor adaptation is sensory error. The algorithm proposed here shows, for the first time to our knowledge, how a sensory-error signal could be used in the general case.

In summary, the present model is unique in its formally proven ability to solve the generic plant compensation problem. It does so using only physically obtainable signals, and it exploits features of cerebellar architecture that are otherwise puzzling, namely recurrent mossy-fibre inputs and sensory CF inputs.

One final issue concerns the role of the visual and vestibular inputs to the flocculus, referred to in § 3*a*. These would appear to be useful for adaptation, not to changes in the plant that affect all types of eye movement, but to changes in (for example) the signal from the semicircular canals, which concerns only a specific subset of eye movements. When it is the plant that needs compensation, these specific inputs will be more weakly correlated with retinal slip than will the inputs indicating eye-movement commands, and the latter will dominate learning.

(c) *Predictions of the model*

The most important feature of our algorithm is that it addresses a potential weakness in Marr–Albus models, namely their apparent reliance on the unavailable signal of motor error. The issue of getting these models to work in practice was apparent to Marr himself, when he commented '.. the [1969] study disappointed me, because even if the theory was correct, it did not much 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). From this point of view the present study is explanatory rather than predictive, though it could be said to 'predict' the ubiquity of recurrent connections and the presence of sensory information in the putative teaching signal.

In the specific context of oculomotor plant compensation, the model predicts the presence of an eye-position-related output from floccular PCs. Such output has been identified in a subset of these cells (the flocculus has functions besides plant compensation, see references in Dean *et al.* (2002)). More detailed predictions of floccular output require precise specification of the brainstem controller *B* and the oculomotor plant *P* (figure 2). It is possible that the properties of *B* and *P* combined could be inferred from the effects of floccular inactivation; the properties of *P*, which are more complex than often assumed (Robinson 1981; Sklavos *et al.* 2003), require multiple techniques to identify.

(d) *Functional role for recurrent connectivity*

The importance of recurrent cerebellar connectivity was emphasized by Eccles (1969) who called this architecture the cerebellar 'dynamic loop'. Experimental evidence for recurrent motor pathways has steadily accumulated (e.g. Holdefer *et al.* 2000) and they are widely regarded as a generic property of motor systems (Middleton & Strick 2000). For example one reviewer asserts that '...multiple closed-loop circuits appear to be a major functional unit of cerebrocerebellar circuitry' (Dum & Strick 2003, p. 637) and another asserts that 'we can now see closed cerebro-cerebellar loops that include sensorimotor regions, and prefrontal regions' and remarks that 'all we need to do now is work out what they are for!' (Ramnani & Miall 2001, p. 136).

We have provided a possible answer. An elegant functional role for these cerebellar loops is that they allow stable adaptive learning using only observable sensory error, with consequent advantages for the modularity of micro-zone connectivity. This allows the cerebellar microcircuit to be treated as a 'cerebellar chip', which can be plugged into a motor system to improve performance, without the need for complex hard-wired back-up structures to ensure compatibility between sensory and motor representations. Such generality should allow the proposed algorithm to compensate for virtual plants, an
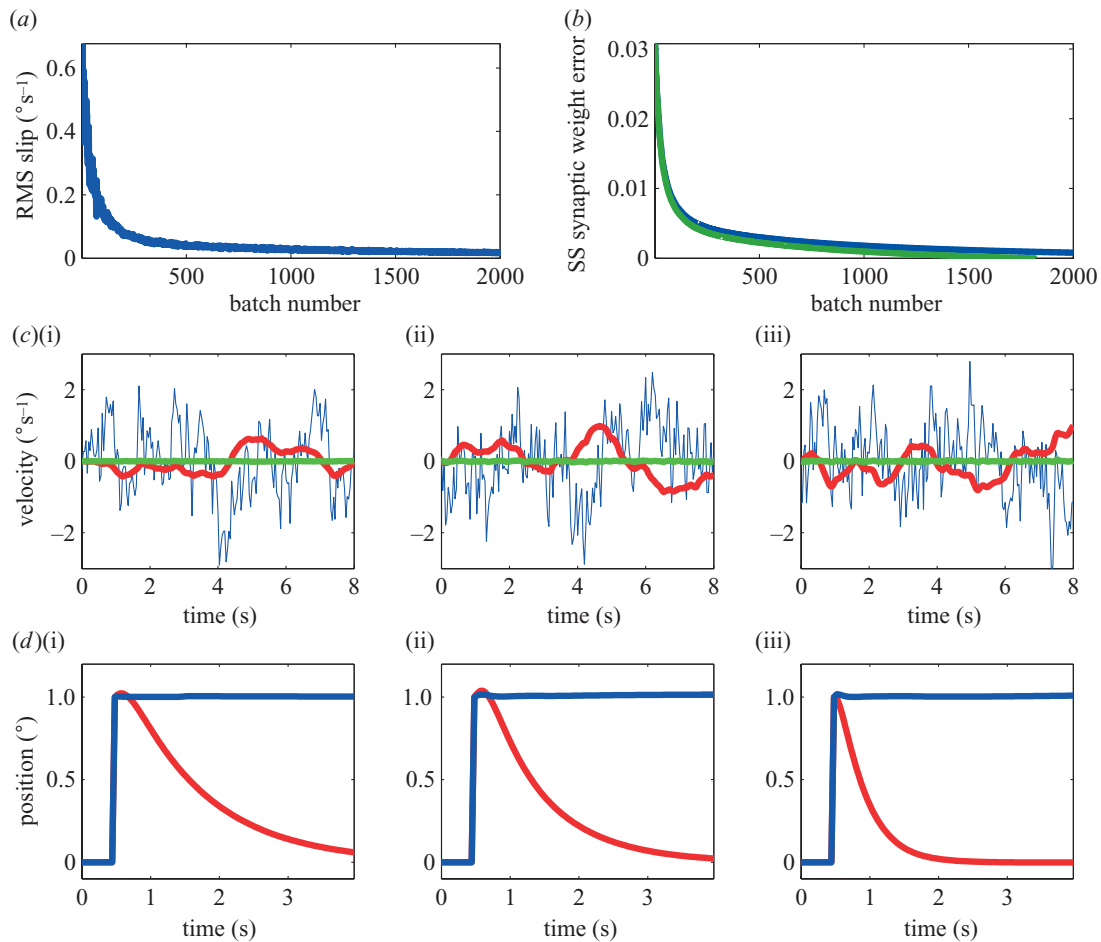
Figure 4. 3D VOR simulation (MatLab code is available from the authors). The oculomotor plant was modelled as a 3×6 array of leaky integrator transfer functions $P(s) = P^0 s/(s + 1/T)$ (pulling directions and strengths of individual muscles are described by the matrix P^0, their dynamic characteristics are described by the innervation-to-velocity transfer function $s/(s + 1/T)$, $T = 0.2$ s). The brainstem contribution was modelled as a 6×3 array of transfer functions $B_{ij} = B_{ij}^0 + B_{ij}^1/(s + 1/T_{ij})$ with correct high frequency gain (so $P^0 B^0 = 1$); time constants T_{ij} were randomly chosen between 0 and 1 s. This reproduced the characteristic low-frequency deficit of the VOR after cerebellar lesions (Zee *et al.* 1981). Granule cell transfer functions were modelled as delay lines $G_i(t) = \delta(t - t_i)$ with a maximum delay of 2 s. During training, head angular velocity was modelled as coloured noise with a spectral exponent of 1. The discretization time was 0.02 s and for efficiency weight update took place in 10 s batches. (*a*) Root mean square (RMS) retinal slip error plotted against batch number; this tends stochastically to zero as predicted by theory. (*b*) Sum of the squares (SS) of synaptic-weight error plotted against batch number (blue curve). This error decays monotonically at the rate predicted by theory (green curve) (the slight discrepancy between the two curves is caused by discretization and the use of batch rather than continuous updates). (*c*) The (i) horizontal, (ii) vertical and (iii) torsional components of response to a coloured-noise input. Head motion is shown in blue, retinal slip before training in red and after training in green. (*d*) The (i) horizontal, (ii) vertical and (iii) torsional responses to a step change in all three components of head position: before training (red) an initial change in head position of the correct magnitude is followed by a decay to the primary position; after training (blue) the correct step response is obtained.

ability perhaps relevant to learning how to use prostheses driven directly by neural activity (Nicolelis 2003).

APPENDIX A

We present a proof of convergence in the linear case (although the proof extends, at least formally, for problems where B, P and G_i are nonlinear operators). We use the deterministic approach based on continuous update (Sastry & Bodson 1989) (proof using stochastic methods is also possible).

For multidimensional problems the cerebellar filter $C = \Sigma w_i G_i$ is a matrix operator and the coefficients w_i are matrices. The learning rule (figure 1, legend) can be written in matrix form as

$$\dot{w}_i = -\beta \, e \, p_i^T$$

(where the signals e and $p_i = G_i * y$ are vectors). Following the flow diagram in figure 2*b* from y to x we see that, for all signals y in the range of B:

$$x = (B^{-1} - C)y = B^{-1}y - \sum w_i p_i,$$

where B^{-1} is any left inverse of B (which we assume to exist). To simplify the argument we also assume that the representation p_i produced by the granule cell layer is

sufficiently rich that there are correct synaptic weights w_i^* for which $\hat{x} = x$, so that

$$\hat{x} = (B^{-1} - C^*)y = B^{-1}y - \sum w_i^* p_i.$$

Taking the difference of these last two equations allows us to relate output error to synaptic-weight error

$$e = \hat{x} - x = \sum (w_i - w_i^*) p_i.$$

Introducing sum square synaptic weight error

$$V = \frac{1}{2}\sum \|w_i - w_i^*\|^2 = \frac{1}{2}\mathrm{tr}((w_i - w_i^*)(w_i - w_i^*)^T),$$

as a Lyapounov function we find that

$$\dot{V} = \sum \mathrm{tr}((w_i - w_i^*)\dot{w}_i^T) = -\beta \sum \mathrm{tr}((w_i - w_i^*) p_i e^T)$$
$$= -\beta \sum \mathrm{tr}(e^T(w_i - w_i^*) p_i) = -\beta \mathrm{tr}(e^T e),$$

(where tr is the trace operator), so that

$$\dot{V} = -\beta \|e\|^2.$$

This remarkable equation shows that the rate of decrease of sum square synaptic weight error is directly proportional to sum square output error. That is synaptic weights are improved whenever errors are made. Its simple form allows us to derive a convergence lemma without appealing to the usual Lyapounov machinery (Sastry & Bodson 1989).

Lemma A.1. *The root mean square sensory error*

$$e_{\mathrm{rms}}^T(t) = \sqrt{\frac{1}{T}\int_t^{t+T} \|e\|^2}$$

over an interval $[t, t+T]$ *tends to zero as* $t \to \infty$.

Proof. If this were not the case then $V(t) = V(0) - \beta \int_0^t \|e\|^2$ would eventually become negative, which is impossible. ∎

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