

IS THE CEREBELLUM AN ADAPTIVE FILTER?

M. G. PAULIN*

Department of Zoology, University of Auckland, New Zealand

(Received August 21, 1985)

Abstract

Fujita's adaptive filter model of cerebellar control of the vestibulo-ocular reflex is inconsistent with empirical data on the behavior of the reflex. The model provides further evidence against the "Marr-Albus" theory of cerebellar function and the flocculus hypothesis of vestibulo-ocular reflex control.

1. Introduction

More than fifteen years have passed since David Marr (1969) published his theory of cerebellar function. James Albus (1971) independently developed a similar theory. Today, the idea that climbing fibers act as "teachers" in the adjustment of parallel fiber-Purkinje cell synaptic weights according to an associative learning rule is known as the Marr-Albus theory of cerebellar function. A prediction of this theory is that permanent changes in Parallel fiber-Purkinje cell synaptic strength occur when there is a temporal correlation between climbing fiber and parallel fiber inputs to a Purkinje cell. For many years, attempts to measure such a phenomenon gave equivocal results: No effect was observed, but the possibility could not be discounted that this was due to a lack of sensitivity of the measurement apparatus, or some other confounding effect. Although the Marr-Albus theory is an elegant and attractive one, it began to receive increasing criticism (Llinas, 1981). Recently, however, it has been reported that observations of "heterosynaptic plasticity" in the cerebellar cortex have been made (Ito, Sakurai and Tongroach, 1982), and it has been asserted that these observations support the Marr-Albus theory (Ito, 1984).

The Marr-Albus theory describes a spatial pattern recogniser. It explains how Purkinje cells can learn to recognise particular patterns of sensory inputs ("context") and generate appropriate movements in response. Experimentalists realised that this is not sufficient to account for dynamical control of movements, and that a dynamical systems or control theoretic model is required (Ito, 1981). The Marr-Albus theory has been reformulated in a control theoretic framework by Fujita (1982a), who has

*Present address: Department of Otolaryngology — Head and Neck Surgery, University of Southern California, Los Angeles CA 90033, U.S.A.

modeled the cerebellar cortex as an adaptive filter. Adaptive filters are used by engineers to control or observe processes whose dynamics are time-varying in an unpredictable way. The idea is that the required control signal is approximated by a linear combination of fixed signals, and the weights of the linear combination are adjusted on-line by an error feedback system to optimise some measure of overall system performance. Fujita's computer simulations (Fujita, 1982b) are in excellent agreement with experimental data, and this is held to be strong supporting evidence for the "Marr-Albus-Fujita" model (Ito, 1984).

2. An Adaptive Filter

If A_1, A_2, \dots, A_n is a set of operators then $\sum_{i=1}^n w_i A_i$ is an operator, and the operation it performs can be varied by varying the weights w_1, w_2, \dots, w_n . This can be implemented physically by an array of elements corresponding to A_1, \dots, A_n , whose outputs are summed. Suppose that the array is required to perform some filtering task, and we do not know in advance what operation is required, but we have some way of measuring, during operation, how well it is performing the task. There are a number of ways in which the weights w_1, w_2, \dots, w_n can be adjusted automatically so as to optimise the performance of the filter. The most obvious automatic system is to have a computer do a recursive grid search, i.e. measure performance as the weights are varied systematically around their current values, adjust them to the point which gives the best performance, and then repeat the search around the new point. Very efficient search procedures can be based on this simple principle (e.g. the simplex algorithm, Nedler and Mead, 1965). A more sophisticated approach is to attempt to estimate the local gradient of the performance index as a function of the weights, and then adjust the current weight vector in the direction of greatest improvement in performance ("steepest descent"). Whichever way the parameter adjustment is achieved, the effect is that the parameter vector of weights moves gradually "downhill" on the graph of system performance and approaches the point of optimal performance (Astrom and Eykoff, 1971). An array filter which can automatically seek and track optimal parameter sets is called an adaptive array filter (Brandwood and Tarran, 1982).

The adaptive filter model of the cerebellar cortex proposed by Fujita (1982a) uses a familiar parameter tracking method known as feedback correlation (Brandwood and Tarran, 1982). In this method, each weight is adjusted at a rate proportional to the correlation between the input to its corresponding operator and the error in filter output. Thus, if there is a positive correlation between error and the signal passing through the i th element, then the contribution of the i th element to the filter output is reduced, and vice-versa. This is a dynamic version of the associative learning rule used in the Marr-Albus theory. Formally, let the filter output be

$$(1) \quad \hat{x}(t) = \sum_{i=1}^n w_i u_i$$

where u_i is the unity-gain output of the i th filter element and let the error signal be

$$(2) \quad e(t) = \hat{x}(t) - x(t);$$

i.e. the difference between actual (\hat{x}) and desired (x) output from the filter. The mean squared error in performance in the last T time units is

$$(3) \quad V(w_1, \dots, w_n; t) = \frac{1}{T} \int_{t-T}^t e^2(s) ds.$$

Now, the gradient of V with respect to the weights w_1, \dots, w_n has components

$$(4) \quad \frac{\partial V}{\partial w_j} = \frac{2}{T} \int_{t-T}^t e(s) u_j(s) ds,$$

and the right hand side of (4) is an estimate of the covariance of the filter output error and the input to the j th filter element. Thus, the filter will automatically seek the parameter set w_1, \dots, w_n which minimises the mean squared error index (V) if the rate of change of the j th input gain is proportional to minus the covariance of the j th input and the error. This is a very efficient optimisation method, used by engineers for high performance adaptive array filters (Brandwood and Tarran, 1982).

Unfortunately, feedback correlation adaptive filters are sensitive to the quality of the error feedback signal. As a specific example, suppose that the array inputs and the array output are sinusoids with frequency w Hz. Now suppose that there is a time delay of $1/2w$ seconds in the error feedback loop. This half cycle delay means that the error report arriving at the correlator is *minus* the true error, the gradient estimate computed by the correlator points in the opposite direction to the true gradient, and the mechanism causes the parameter set to track directly *away* from the optimal parameter point. In fact, if there is a delay in the error feedback signal which exceeds $1/4w$ seconds then the feedback correlation mechanism is counter adaptive, because the quarter cycle delay makes the reported error signal negatively correlated to the true error at any time.

When the values of system gain and phase parameters during learning are mapped in the complex plane (as in Fujita, 1982b) then a phase shift of p degrees in the error feedback signal will swing the gradient estimate produced by the correlator to an angle p degrees from the true gradient. This is easily verified by introducing an extra phase error term $\exp(ip)$ into the gradient computation using transfer function notation (Fujita, 1982b; equation 2.3). Thus, a phase shift of less than 90 degrees will cause the parameter set to slow its approach to the optimal point, and it will not travel along a steepest descent path of the performance index. If there is a phase shift of 90 degrees or greater, then the parameter set will move steadily *away* from the point which minimises mean squared error, along a spiral trajectory in the complex plane.

If there is a time delay of D seconds in the error feedback loop, then the feedback correlation mechanism is counter-adaptive at frequencies above $1/4D$ Hz.

3. The Vestibulo-Ocular Reflex

When the head rotates, the eyes counter-rotate and the retinal image is held relatively steady. During slow head movements the accuracy of compensatory movements is ensured by an image-slip feedback loop from the retina to the extraocular muscles. The eye reflex response to background image movement is called the optokinetic reflex (OKR). If there is an unpredictable image movement with frequency components above only about 1 Hz, then the human OKR cannot maintain clear vision (Carpenter, 1977). During head rotation at higher frequencies, compensatory eye movements are generated by the vestibulo-ocular reflex (VOR). Because the VOR is an open-loop control system it must be calibrated so that the reflex movements compensate for the head movement. Shortly after Marr and Albus published their theories of cerebellar function, Ito noted that the VOR provides an ideal case study for testing the validity of these theories (Ito, 1984). Ito proposed the "flocculus hypothesis" of vestibulo-ocular reflex control, according to which retinal image slip signals arriving at the cerebellar cortex via climbing fibers provide an error signal for Purkinje cells which lie on a side-arc of the vestibulo-ocular reflex. The Marr-Albus theory describes how these Purkinje cells may then learn how to respond so that eye movements minimise retinal image slip during head movements. Fujita (1982b) has translated the flocculus hypothesis into the language of control theory, using his adaptive filter model of cerebellar function (Ito, 1984).

In humans, there are significant head movements at frequencies above 1 Hz (Skavenski, Hansen, Steinman and Winterson (1979)). In view of this, we might ask why the automatic calibration property of feedback control systems is applied over only a part of the physiological band of the eye stabilisation system, i.e. the d.c. to 1 Hz band in which the OKR is effective. It has been claimed that this is because there is a time lag in the retinal image slip signal, and that this time lag would make feedback ineffective — indeed, counter-productive — if the closed loop response were not attenuated in the upper part of the physiological band (Robinson, 1976). Therefore, an open-loop control system must be used.

Robinson (1976) claims that there is a delay of at least 70 msec in optokinetic feedback to the extraocular motor system. Carpenter (1977) gives the same figure. Dallos and Jones (1963) estimated that the delay must be about 70 msec, as did St. Cyr and Fender (1969). Collewijn (1975) measured image slip latencies in the rabbit's nucleus of the optic tract with average latencies of 60 ± 10 msec, and argues that the closed loop delay in the rabbit optokinetic reflex is more than 80 msec (Collewijn, 1979). Barmack and Hess (1980) measured latencies to visual image slip in the inferior olive, which is the source of climbing fibers to the inferior olive, at between 40 and 180 msec.

With an error feedback delay of 70 msec, the feedback correlation mechanism is counter-adaptive at frequencies above $1/(4 \times 0.070) = 3.6$ Hz. Feedback correlation therefore cannot be used to tune the VOR above 3.6 Hz, but recent measurements show that the VOR is accurate at considerably higher frequencies. Hyden, Larsby and Nykqvist (1984) measured the human VOR in the band 0.2–4.25 Hz, and found that it gives excellent compensation at the upper limit. Reker (1984) measured com-

pensatory eye movements up to 15 Hz, and concluded that the human VOR is probably effective to at least 10 Hz. Benson (1971) measured approximately unity gain in the human VOR up to about 8 Hz. Skavenski, Hansen, Steinman and Winterson (1979) found that the human VOR gives good compensation up to about 15 Hz. Gauthier, Piron, Roll, Marchetti and Martin (1984) showed that the human VOR is compensatory up to 15 Hz, and there is negligible phase error below 6 Hz. Stott (1984) measured compensatory VOR responses up to over 30 Hz.

There is a similar pattern in results from animal experiments. Keller (1978) measured the monkey VOR and found a strong response up to 8 Hz. Winterson, Collewijn and Steinman (1979) give data showing that the rabbit VOR actually improves with increasing frequency up to at least 10 Hz. Furman, O'Leary and Wolfe (1979) measured the monkey VOR to 5 Hz and found that the reflex is strong at the upper tested frequency.

4. The Adaptive Filter Model

The upper band limit of effective compensatory eye movements produced by the open-loop human VOR is too high for it to be possible that the VOR is calibrated by a feedback correlation mechanism, because of the time delay in retinal image slip feedback. A conservative estimate of the VOR upper band limit based on modern data (say, 10 Hz) places it at least an octave (factor of two) above the upper frequency limit imposed by a conservative estimate of the delay in retinal image slip feedback (say, 50 msec).

Computer simulations of learning behaviour of the adaptive filter model (Fujita, 1982b) give results in good agreement with experimental data. The steepest descent property of parameter changes during learning had not been noted by experimentalists, and the demonstration of this effect is significant because it represents a true prediction based on a theoretical model. However, this is a *generic* property of adaptive (recursive, self-tracking) systems (Astrom and Eykoff, 1971), and the observation that reflex parameters do seem to follow a steepest descent path of a performance index during learning should not be interpreted as support for the particular adaptive filter model proposed by Fujita (1982a). Indeed, the prediction was made independently, on the basis of a different model, by Paulin (1982). This observation suggests only that some kind of systematic error tracking mechanism is involved in VOR adaptation.

It is most important to remember that an observation does not support a theory unless it can be shown, or reasonably assumed, that the observation is impossible or unlikely if the theory is false. In the present case, any error-tracking control system which actually works seems likely to exhibit the steepest descent property. To discover exactly what kind of mechanism(s) are involved, we must exploit the *differences* between alternative possibilities. Here, this has led to an investigation of time delays in the feedback loop, because the feedback correlation mechanism fails if there is a sufficiently large time delay. This leads to rejection of the adaptive filter model proposed by Fujita (1982a,b).

An alternative adaptive filter mechanism, and one which is effective despite error feedback delays, is parameter perturbation (Brandwood and Tarran, 1982). In this method, the weights are subject to small perturbations which generate corresponding small variations in filter performance. The covariance of the value of a particular parameter and the filter performance index is an estimate of the gradient of the performance index with respect to that parameter. Thus, if the mean value of each parameter evolves at a rate proportional to minus its covariance (or correlation) with filter performance, then the filter evolves towards optimal performance. This is a stochastic "natural" version of the grid search mechanism, and an automatic version of the method a person might use to adjust unlabelled controls on some device — i.e. move the controls at random and see which adjustments tend to improve performance of the device. Parameter perturbation is candidate mechanism for adaptive modification of the VOR.

5. The Flocculus Hypothesis

The flocculus hypothesis can be defended by disassociating it from the adaptive filter model, but a variety of experimental results have cast doubt on the validity of the hypothesis.

Experiments in which the cerebellar cortex is removed without damage to underlying structures suggest that the cortex is *not* necessary for recovery and maintenance of vestibular reflex function after lesions (Haddad, Freindlich and Robinson (1977); Llinas and Walton (1979); Schaefer and Meyer (1981); Courjon, Flandrin, Jeannerod and Schmidt (1982)). In rats which have been allowed to recover from the effects of unilateral vestibular lesion, temporary chemical lesion of the inferior olive causes a reappearance of the original symptoms of the lesion (Llinas, Walton, Hillman and Sotelo 1975; Demer and Robinson, 1982). It seems difficult to reconcile this result with any theory which suggests that the recovery is due to learning which occurs solely or principally in the cerebellar cortex. But it is possible that the inferior olive somehow facilitates the operation of Purkinje cells and that their learned responses are simply not expressed when the olive is disabled. Ito, Nisimaru and Shibuki (1979) presented data suggesting that this is indeed the case, however Montarolo, Raschi and Strata (1981) failed in an attempt to confirm this.

It has been considered vital for the Marr-Albus theory and for the flocculus hypothesis, to demonstrate the occurrence of long term changes in parallel fiber-Purkinje cell synaptic strength associated with correlated climbing fiber-parallel fiber input to a Purkinje cell. Success has recently been announced (Ito, Sakurai and Tongroach, 1982; Ekerot and Kano, 1983; Ito, 1984). However, the "long term" modification described by Ito, Sakurai and Tongroach (1982) lasts for only ten minutes, with a secondary effect which becomes unmeasurably small within about one hour. The claim by these authors that this result is consistent with the Marr-Albus theory is surely an overstatement, because the theory describes permanent changes

which are supposed to be affected only by subsequent relearning. An attempt by Llinas and Sugimori (1980), using more sensitive intracellular methods, failed to discover any evidence of such an effect. Ito (1984) has suggested that this failure might be due to a methodological fault.

Even if the observation made by Ito, Sakurai and Tongroach (1982) is consistent with the Marr-Albus theory, as the authors claim, it is *not* true that the observation supports the Marr-Albus theory as claimed by Ito (1984). The question is, what might we expect to observe if the Marr-Albus theory (or the flocculus hypothesis) were false? If it cannot be shown or reasonably argued that the experimental results are impossible or unlikely if the theory is wrong, then it cannot be claimed that the results are evidence in favour of the theory.

6. Conclusion

The adaptive filter model presented by Fujita (1982a) is an interesting step towards a multivariate control theoretic model of movement control, and the role which the cerebellum plays. The time-delay argument presented in this paper shows, however, that the behaviour of this model is inconsistent with empirical results. The model provides limited insight into the deceptively simple problem of VOR calibration. Similarly, the Marr-Albus theories and the flocculus hypothesis have received no substantive empirical support since they were formulated. The cerebellum — what it does and how it does it — remains an enigma.

References

- Albus, J. S. (1971). A theory of cerebellar function. *Math. Biosci.* **10**, 25–61.
- Astrom, K. J. and Eykoff, P. (1971). System identification — a survey. *Automatica* **7**, 123–162.
- Barmack, H. H. and Hess, D. T. (1980). Multiple-unit activity evoked in dorsal cap of inferior olive of the rabbit by visual stimulation. *J. Neurophys.* **43**, 165–181.
- Benson (1971). Compensatory eye movements produced by angular oscillation. *Proc. XXV IUPS* **9**, 149, Munich.
- Brandwood, D. H. and Tarran, C. J. (1982). Adaptive arrays for communications. *Proc. IEE F* **129**, 223–232.
- Carpenter, R. H. (1977). *Movements of the eyes*. Pion, London.
- Collewijn, H. (1975). Direction-selective units in the rabbits nucleus of the optic tract. *Brain Res.* **100**, 489–508.
- Collewijn, H. (1979). The modifiability of the adult vestibulo-ocular reflex. *TINS* **1**, 98–102.
- Constantine-Paton, M. (1983). Convergent activity patterns: Can they alter axon trajectories? *TINS* **6**, 441–442.
- Courjon, J. H., Flandrin, J. M., Jeannerod, M. and Schmidt, R. (1977). The role of the flocculus in vestibular compensation after hemilabyrinthectomy. *Brain Res.* **239**, 251–257.
- Dallos, P. J. and Jones, R. W. (1963). Learning behavior of the eye fixation control system. *IEEE AC-8*, 218–227.
- Demer, J. L. and Robinson, D. A. (1982). Effects of reversible lesions and stimulation of the olivocerebellar system on vestibulo-ocular plasticity. *J. Neurophys.* **47**, 1087–1107.
- Ekerot, C-F. and Kano, M. (1983). Climbing fiber induced depression of Purkinje cell responses to parallel fiber stimulation. *Proc. IUPS* **15**, 393, Sydney.
- Fujita, M. (1982a). Adaptive filter model of the cerebellum. *Biol. Cyb.* **45**, 195–206.
- Fujita, M. (1982b). Simulation of adaptive modification of the vestibulo-ocular reflex with an adaptive filter model of the cerebellum. *Biol. Cyb.* **45**, 207–214.
- Furman, J. M., O'Leary, D. P. and Wolfe, J. W. (1979). Application of linear systems analysis to the horizontal vestibulo-ocular reflex in the alert rhesus monkey using pseudorandom binary sequence and single frequency sinusoidal stimulation. *Biol. Cyb.* **33**, 159–165.
- Gauthier, G. M., Piron, J., Roll, J., Marchetti, E. and Martin, B. (1984). High frequency vestibulo-ocular reflex activation through forced head rotation in man. *Aviat. Space and Environ. Med.* **55**, 1–7.
- Haddad, G. M., Freindlich, A. R. and Robinson, D. A. (1977). Compensation of nystagmus after VIIIth nerve lesions in vestibulocerebellectomised cats. *Brain Res.* **135**, 192–196.
- Hyden, D., Larsby, B. and Odkvist, L. M. (1984). Quantification of eye movements in light and darkness. *Acta Otolaryngol.* **S406**, 209–211.
- Ito, M. (1981). Experimental verification of Marr-Albus plasticity assumption for the cerebellum. *Acta. Biol. Hung.* **33**, 189–199.
- Ito, M. (1984). *The cerebellum and Neural control*. Raven, NY.
- Ito, M., Nisimaru, N. and Shibuki, K. (1979). Destruction of inferior olive induces rapid depression in synaptic action of cerebellar Purkinje cells. *Nature* **277**, 568–569.
- Ito, M., Sakurai, M. and Tongroach, P. (1982). Climbing fiber induced depression of both mossy fiber responsiveness and glutamate sensitivity of cerebellar Purkinje cells. *J. Physiol. (Lond.)* **324**, 113–134.
- Keller, E. L. (1978). Gain of the vestibulo-ocular reflex in monkey at high rotational frequency. *Vision Res.* **18**, 311–315.
- Llinas, R. R. (1981). Cerebellar Modeling. *Nature* **291**, 279–280.
- Llinas, R. R. and Sugimori, M. (1980). Electrophysiological properties of in vitro Purkinje cell somata in mammalian cerebellar slices. *J. Physiol.* **305**, 171–195.
- Llinas, R. R. and Walton, K. (1979). Vestibular compensation: A distributed property of the central nervous system. In *Integration in the nervous system*. Asunama, H. and Wilson, V. J. (eds). Igaku-Shoin Tokyo. pp. 145–166.
- Llinas, R. R., Walton, K., Hillman, D. E. and Sotelo, C. (1975). Inferior olive: Its role in motor learning. *Science* **190**, 1230–1231.
- Marr, D. (1969). A theory of cerebellar cortex. *J. Physiol.* **202**, 437–470.
- Montarolo, P. G., Raschi, F. and Strata, P. (1981). Are the climbing fibers necessary for Purkinje cell inhibitory action? *Exp. Brain Res.* **42**, 215–218.
- Nedler, J. A. and Mead, R. (1965). A simplex method for function minimisation. *Computer J.* **7**, 308–313.
- Paulin, M. G. (1982). Cerebellum: Adaptive filter in the brain? *Proc. NZ Physiological Soc.* **2**, 30.
- Reker, U. (1984). The high-frequency limit of the fundamental vestibulo-ocular reflex. *Arch. Oto-rhino-laryngol.* **239**(3), 229–234.
- Robinson, D. A. (1976). Adaptive gain control of the vestibulo-ocular reflex by the cerebellum. *J. Neurophys.* **36**, 954–969.
- Schaefer, K. P. and Meyer, D. L. (1981). Aspects of vestibular compensation in guinea pigs. In *Lesion induced neuronal plasticity in sensorimotor systems*. Flohr, H. and Precht, W. (eds). Springer-Verlag, Berlin, Heidelberg, New York. pp. 197–205.
- Skavenski, A. A., Hansen, R. M., Steinman, R. M. and Winterson, B. J. (1979). Quality of retinal image stabilisation during small natural and artificial body rotations in man. *Vision Res.* **19**, 675–683.
- St. Cyr, G. J. and Fender, D. H. (1969). Nonlinearities of the human oculomotor system: Time delays. *Vision Res.* **9**, 1491–1503.
- Stott, J. (1984). The vertical vestibulo-ocular reflex and ocular resonance. *Vision Res.* **24**, 949–960.
- Winterson, B. J., Collewijn, H. and Steinman, R. M. (1979). Compensatory eye movements to miniature rotations in the rabbit: Implications for retinal image stability. *Vision Res.* **19**, 1155–1159.