ebellum including the flocculus in rabbits¹¹, cats¹² and monkeys¹³, or subdural application in rabbits and monkey of haemoglobin (which blocks LTD)¹⁴, abolishes the entire VOR adaptation, raises the question of why brain stem synaptic plasticity does not show up in the absence of cerebellar plasticity.

Finally, Purkinje cell responses inconsistent with the flocculus hypothesis in monkeys⁴ and goldfish¹⁵ have been observed under visual cancellation of the VOR. Such responses would be free of eye-velocity signals, but at the same time would be contaminated by visual signals or higher command signals acting to cancel the VOR. The signal contents of these responses need careful reconsideration before they can be related to VOR adaptation.

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LISBERGER AND SEJNOWSKI REPLY — We are surprised that Ito is so strongly opposed to a model that accounts for his data and ours, and that allows the cerebellar cortex of the flocculus and/or the ventral paraflocculus to be one of two sites of learning in the VOR. We also find that Ito's response to our Letter¹ contains some omissions and errors that undermine his position.

(1) Ito claims that Watanabe⁶ and Miles *et al.*⁴ recorded from different Purkinje cells in different parts of the cerebellum. He fails to mention that the two studies recorded in common from at least two folia in the ventral paraflocculus and he fails to cite the fact that individual Purkinje cells in these folia show the same effects reported by both groups¹⁶. Therefore neither group's data can be discounted and any model of the VOR must account for both sets of results. Our model does, and the 'flocculus hypothesis' does not.

(2) Ito does not mention evidence that the earliest expression of learning in the VOR evoked by an electrical stimulus in the labyrinth occurs only 5 ms after the stimulus, too soon to allow time for transmission through the cerebellum¹⁷. He does not cite the existence of a group of cells in the brain stem that express learning 12 ms after the onset of head motion, before most Purkinje cells in the cerebellum show any response¹⁶.

(3) Ito incorrectly explains why our model requires sites of learning in the vestibular inputs to both the cerebellum and the brain stem. Our model requires two sites of learning so that constant head velocity can generate constant eye velocity. If learning is localized in just one site in the cerebellar or the brain stem pathway, then a constant head velocity generates an eye velocity that

ramps inexorably toward positive or negative infinity. This behaviour is a consequence of the structure of the model and of the fact that the model processes inputs and generates outputs that vary as a function of time. The need for two sites of learning is unrelated to the exact mechanism of learning and, in fact, the form of long-term depression supported by Ito could be a mechanism of learning in our model.

(4) In defending the 'flocculus hypothesis', Ito fails to cite a study done in rabbits showing that motor learning in the VOR can be acquired without vestibular stimulation¹⁸. This study contradicts the 'flocculus hypothesis', which requires activation of vestibular inputs during motor learning.

Our model, although it requires more than one site of learning, accounts for data from multiple laboratories and reconciles observations that had been thought previously to be contradictory. Even for a relatively simple behaviour like the VOR, a biological system must face many constraints that require a complex neural network with the possibility of multiple sites and mechanisms of learning. The challenge is to elucidate the operation of the whole system, not merely to determine the function of an individual structure or an isolated synapse.

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Palaeoclimate sensitivity

SIR — Those studying global warming generally define climate sensitivity as the response of the globally and annually averaged temperature to a doubling of CO₂. Such a quantity is, in theory, well defined, but to assume that major climate regimes in the past arose from such simple forcing is unjustified. To use past climate to infer sensitivity to a doubling of CO₂, as was done recently by Hoffert and Covey¹, is equally unjustified. In their Fig. 2, both the warmer and colder climates considered may have had tropical temperatures approximately the same as the current climate. But the differences in temperature between the tropics and high latitudes were very different. This, in turn, implies that these past climates were associated with very different north–south dynamic heat fluxes in the atmosphere–ocean system.

Such heat fluxes are important in at least two major respects: first, without them, the annually averaged pole-to-Equator temperature difference for the present climate would be about twice as great as it is². Second, given that the Earth's major greenhouse gas, water vapour, varies greatly with latitude and altitude, it is impossible to calculate the net greenhouse effect without knowing where heat is deposited by the dynamic heat transports³. In addition, the atmospheric contribution to this heat transport is at least as great as that from ocean currents⁴, and is dominated by fluxes in winter⁵.

Dynamic fluxes depend on motions which in turn depend on spatial variations in heating. Thus, orbital variations are believed to have caused the cyclic glaciations of the past 700,000 yr (the Milankovitch hypothesis⁶). These variations involve very small changes in globally and annually averaged insolation, but give rise to major changes in the spatial distribution of heating. Atmospheric fluxes are likely to depend on the intensity of the Hadley circulation in the tropics^{7,8}. This intensity, in turn, depends strongly on the displacement of the zonally averaged summer surface temperature maximum from the Equator⁹, and on the meridional sharpness of the zonally averaged temperature maximum⁸. The former is extremely sensitive to orbital parameters, whereas the latter depends greatly on the nature of monsoons. Monsoons clearly depend on the distribution of land and sea in the tropics; this was certainly very different during the mid-Cretaceous period considered by Hoffert and Covey¹. Incidentally, neither of these two factors depends significantly on gross radiative