Inverse-dynamics model eye movement control by Purkinje cells in the cerebellum

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MANY lines of evidence suggest that the cerebellum is involved in motor control[1]. But what features of these movements are encoded by cerebellar neurons? For slow-tracking eye movements, the activity of Purkinje cells in the ventral paraflocculus of the cerebellum is known to be correlated with eye velocity[2–5] and acceleration[5]. Here we show that the complex temporal pattern of the firing frequency that occurs during the ocular following response elicited by movements of a large visual scene[6–8] can be reconstructed by an inverse-dynamics representation, which uses the position, velocity and acceleration of eye movements. Further analysis reveals that the velocity and acceleration components can provide appropriate dynamic drive signals to ocular motor neurons, whereas the position component often has the wrong polarity. We conclude that these Purkinje cells primarily contribute dynamic command signals.

Figure 1 shows the sample simple spike activity of a Purkinje cell (P cell) in the left ventral paraflocculus of a monkey together with the ocular following response to 65 presentations of a 160 deg s^{-1} downward test ramp of a large random-dot pattern. Responses were aligned with stimulus onset (time 0). From top to bottom, the ensemble average spike response over the 65 trials of this P cell, eye acceleration, velocity and position, and stimulus velocity are shown. The firing rate of this neuron becomes significantly different from the baseline rate 51 ms after the onset of stimulus motion. In the data shown here, the eyes began moving several milliseconds after the onset of the neural responses. To analyse the information represented in the activity of the P cell, a temporal pattern of ensemble average firing frequency of the P cell was reconstructed by the inverse-dynamics representation method[9–11] as follows:

$$f(t-\Delta)=a\cdot e''(t)+b\cdot e'(t)+c\cdot e(t)+d \qquad (1)$$

where $f(t)$, $e''(t)$, $e'(t)$, $e(t)$, Δ are the firing frequency at time t, the eye acceleration, velocity and position at time t, and the

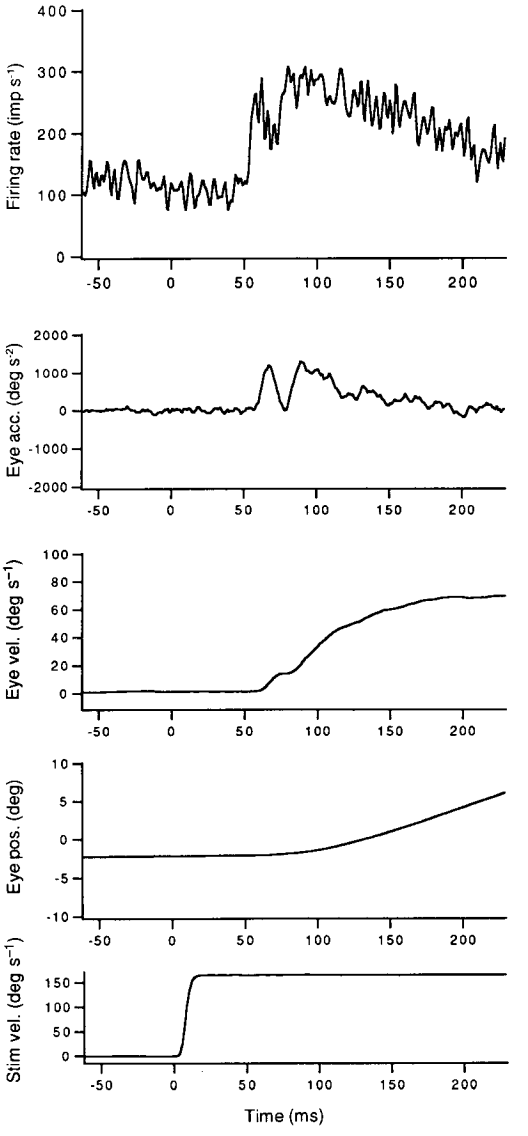

FIG. 1 Simple spike activity of a P cell in the left ventral parafocculus and the ocular following responses to 65 presentations of a 160 deg s^{-1} downward test ramp. Responses are aligned at a stimulus onset (Time 0). From top to bottom: ensemble average firing frequencies, averaged vertical eye acceleration, velocity and position, and averaged stimulus velocity profiles. Upward direction in the figure means downward eye or stimulus movements. All eye-movement data were filtered with a 6-pole Bessel low-pass filter (cut-off, 100 Hz). Latency was 51 ms for unit activity.

METHODS. The animals (*Macaca fuscata*) had been previously trained to fixate a small target spot to obtain a fluid reward. Under Nembutal anaesthesia and aseptic conditions, each monkey was implanted with a cylinder for microelectrode recording, and fitted with a head holder that allowed the head to be fixed in the standard stereotaxic position during the experiments. Scleral search coils were implanted for measuring eye movements[21]. The animals faced a translucent tangent screen (85° × 85° at a distance of 235 mm) on which moving random-dot patterns could be back-projected. The visual stimulus started to move 150 ms after the end of a centering saccade with eight directions at 10–160 deg s^{-1}. Each visual stimulus ramp lasted 250 ms. Voltage signals separately encoding the horizontal and vertical components of eye position, eye velocity, and mirror (stimulus) velocity were digitized to a resolution of 12 bits, sampling at 500 Hz[8]. The acceleration profiles were obtained by digital differentiation of eye velocity profiles after averaging. A time–amplitude window discriminator was used to record spike occurrences with a time resolution of 1 ms.