

Cerebellum-Machine Interface to Understand Cerebellar Roles in Motor Learning

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Abstract—A cerebellum-machine interface (CMI) was developed to understand cerebellar roles in motor control and learning by testing direct causality between single unit cerebellar Purkinje cell activity and motor learning. The CMI converts Purkinje cell simple spike firing rate into pulse-width modulation signals that drive a single joint robot arm. The CMI has no adaptive capability, thus any change observed in robot arm motion can be attributed directly to Purkinje cell firing activity. We employed a vestibuloocular reflex (VOR) adaptation paradigm in goldfish as the test for motor learning. Changes in eye muscle characteristics, or equivalently adding visual motion stimulus during head rotation require oculomotor commands to be calibrated by minimizing image slip across the retina, which acts as a control error signal. This calibration, known as VOR motor learning, has been postulated to depend on synaptic plasticity in the vestibulo-cerebellum, where Purkinje cells are believed to encode motor commands for eye movement. If this is true, then vestibulo-cerebellar Purkinje cells may similarly learn to correct error in a motor command signal when the oculomotor system is replaced with a different system, such as a robot arm. Desired motion and control error signal of the robot arm were presented as head rotation and retinal slip, respectively, to the fish VOR model. The control error of the robot arm was shown to decrease gradually, but not monotonically, and in many cases only in one direction. This evidence is the first direct demonstration that activity of a single Purkinje cell is capable of implementing adaptive motor control. The results also suggest that a single Purkinje cell can be responsible, at least in part, for directional selective VOR motor learning previously reported in goldfish [6] and monkeys [3].

Keywords—goldfish; eye movement; vestibular; Purkinje cell; Brain Machine Interface

I. INTRODUCTION

The cerebellum is intimately involved in motor control and learning as its dysfunction causes ataxia and inability to modify motor behavior. Behavioral and neuro-physiological experiments have demonstrated that cerebellar Purkinje cells change their firing patterns in parallel with adaptive behavioral changes [1][2][4]. However, conventional neurophysiological experiments only indicate the correlation between neural activity and behavior, but do not provide proof of direct causality. Here we developed a cerebellum-machine interface (CMI) to address a direct causality between single

Purkinje cell activity and adaptive behavioral changes in behaving animals. We employed adaptation of the vestibuloocular reflex (VOR) in goldfish to implement and evaluate the CMI. The VOR is an involuntary eye movement utilized to stabilize visual images on the retina during head movement. Both eyes are counter-rotated in the orbit in response to head movement so that VOR gain defined as eye velocity/head velocity ideally approaches unity. If the VOR gain is not calibrated to prevent image slips on the retina, or an external visual stimulus is combined with head movement, then VOR gain is gradually modified so that visual slip is minimized. This motor learning paradigm is the VOR adaptation. Cerebellar floccular Purkinje cells in monkeys [1][2] and vestibulo-cerebellar Purkinje cells in goldfish [4] were shown to change their firing patterns in parallel with VOR adaptation. We connected single unit activity of goldfish vestibulo-cerebellar Purkinje cells to a robot arm via the CMI, and gave control error information to the fish as retinal image slips to see whether a single Purkinje cell being recorded can reduce the control error of the robot arm. We demonstrate that the control error of the robot arm gradually decreased as the firing pattern of the Purkinje cell changed. This evidence is the first direct demonstration that activity of a single Purkinje cell is capable of implementing adaptive motor control.

II. METHODS

A. Animal preparation

Goldfish (*Carassius auratus*), 15cm of standard length, were obtained from an authorized supplier (Meito Suien, Nagoya) and acclimated in well-aerated aquaria at 20 deg. C. At least 2 days in advance, a stainless steel head post was secured onto the frontal bone by dental cement under anesthesia (MS-222, Sigma). At the same time, craniotomy was performed to make a small hole (5mm in diameter) in the occipital bone to access to the vestibulo-cerebellum. The bone flap removed for the craniotomy was placed back and sealed by superglue before putting the goldfish back to its home water tank.

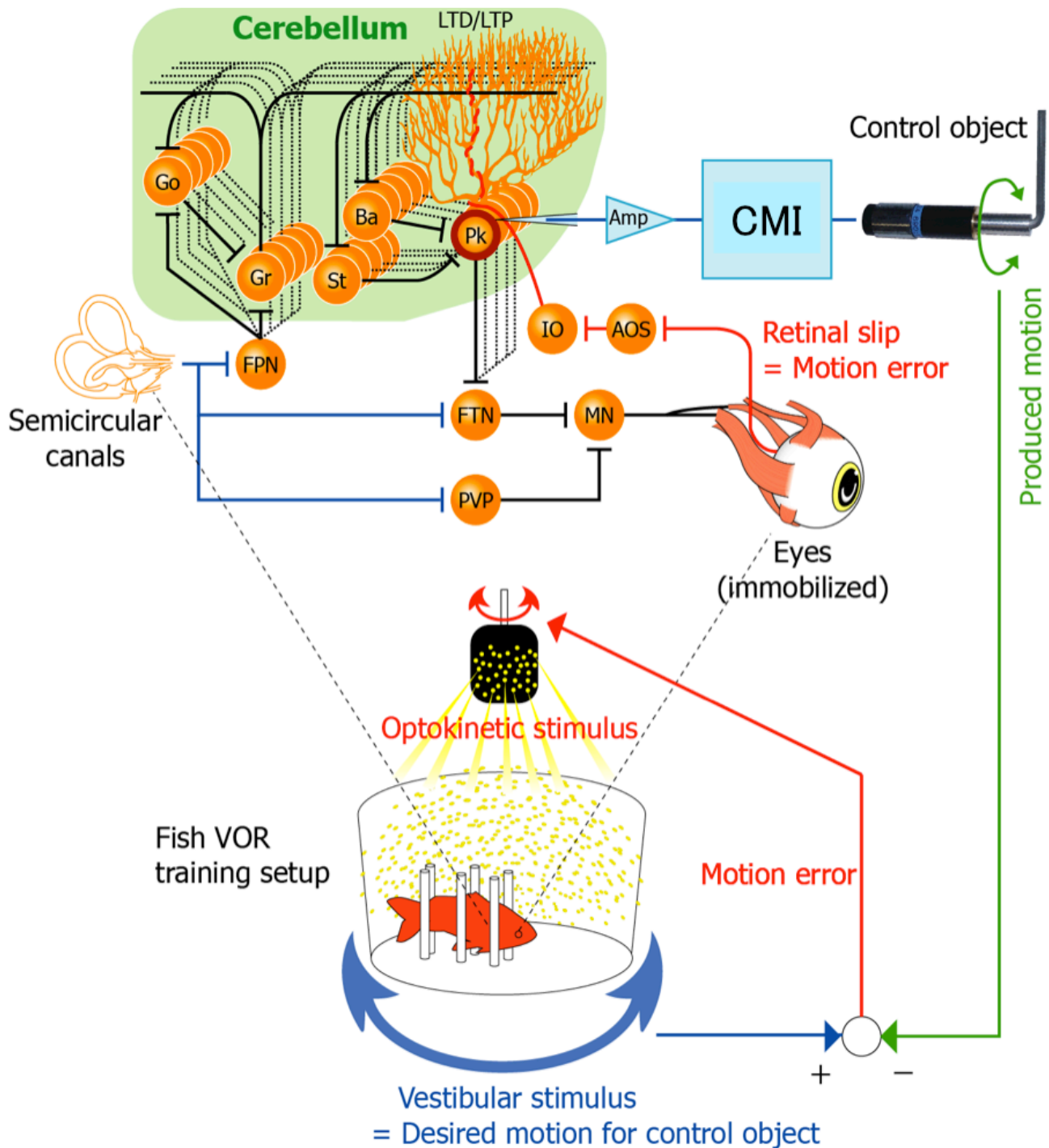


Figure 1: Schematic of direct current motor adaptive control by single unit cerebellar Purkinje cell activity in goldfish via the cerebellum-machine interface (CMI) utilizing a vestibuloocular reflex (VOR) adaptation paradigm. Details of signal processing in the CMI are depicted in figure 2. Go: Golgi cell, Gr: granular cell, St: stellate cell, Ba: basket cell, Pk: Purkinje cell, IO: inferior olive nucleus, AOS: accessory optic system, MN: oculomotor motor neuron, FPN, FTN, PVP: flocculus projecting neuron, flocculus target neuron, position-vestibular-pause neuron, respectively which are from mammalian anatomical evidence (not exactly identified in goldfish). The control object is a direct current motor (RE-max24, maxon).

B. Experimental Setup

Goldfish were gently restrained in a cylindrical aquarium atop a turntable while simple spikes were recorded from single vestibulo-cerebellar Purkinje cells (Fig.1). In the CMI, instantaneous firing rate of the Purkinje cell was calculated and converted into a pulse-width-modulation (PWM) signal to drive a single-joint robot arm attached to a direct current motor. Desired motion for the robot arm was presented to the fish as turntable rotation, and control error of the robot arm (actual motion minus desired motion) was sent to a rotating planetarium projecting a random dot pattern on the aquarium wall (Fig.2). This setup created a visual-vestibular mismatch that induces VOR adaptation in the fish. Notably, in this scheme only the Purkinje cell under recording can reduce the control error. Therefore, if a single Purkinje cell is capable of causing adaptive behavioral change in the VOR, then a change in firing rate should be able to reduce the control error of the robot arm. A sinusoidal wave with the frequency of 0.1Hz was given as a desired motion where positive and negative values were assigned as clockwise (CW) and counter clockwise (CCW) motion of the robot arm, respectively. Spontaneous firing rate of each Purkinje cell was subtracted before converting into PWM signal so that increases and decreases in the firing rate induce CCW and CW robot arm rotation, respectively.

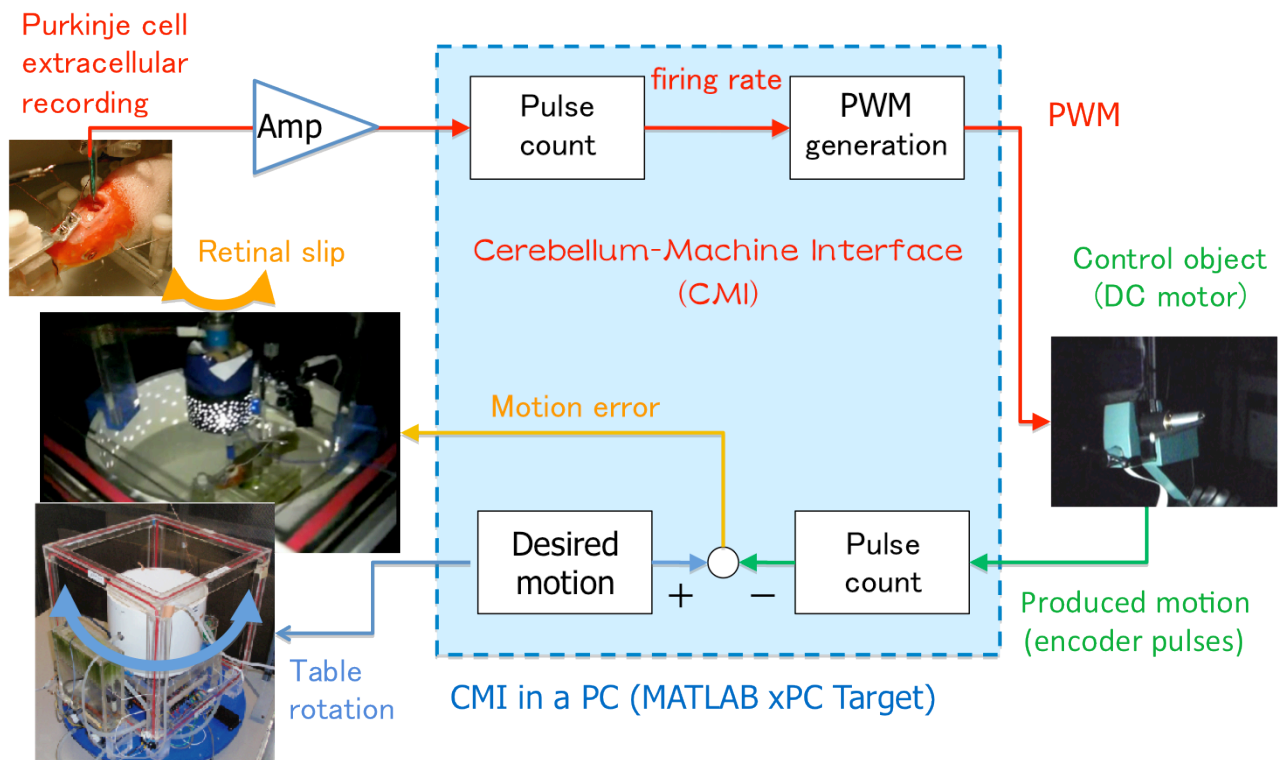
C. Data Analyses

The control errors of the robot arm were averaged over every 10 cycles of the desired motion. In the same way, averaged Purkinje cell firing rates over every 10 cycles of the desired motion were calculated. Further the averaged errors were evaluated separately during CW and CCW motion of the robot arm.

III. RESULTS

Among the different types of vestibulo-cerebellar Purkinje cells that have been identified in goldfish, we employed those having head velocity sensitivity categorized as Head(H)1, H1Eye(E)1, and H1E2 representing 72% of the Purkinje cell population in the area [4]. All Purkinje cells were recorded in the left cerebellum, thus counter-clockwise (CCW) vestibular stimulation corresponds to ipsiversive head rotation (H1). We analyzed Purkinje cell simple spike firing and errors in the robot arm control for the activity of those cells isolated for longer than 10 minutes.

The error in the robot arm control was demonstrated to decrease gradually in 77 % of the isolated Purkinje cells. In all cases in which error decreased, the decline was not monotonic, but rather oscillatory. About half of the Purkinje cells recorded reduced motion error in both on- and off-directions of their firing modulation corresponding to CCW and CW robot arm



VOR motor learning induction setup

Figure 2: The cerebellum-machine interface (CMI) connecting goldfish cerebellar Purkinje cell single unit activities with a direct current (DC) motor. Purkinje cell neural spikes recorded extracellularly are amplified and pulse-counted to calculate instantaneous firing rates. The firing rates are converted into pulse-width-modulation (PWM) signals to drive the DC motor. Produced motion of the DC motor is monitored by counting pulses from its encoder, and compared with the desired motion that is generated in the CMI and fed to the turn table to give the goldfish as vestibular stimulus.

motion, respectively. The other cells only reduced the error in their on-direction and for CCW motion.

IV. CONCLUSIONS

Although single Purkinje cells have been demonstrated to encode motor commands [5], their firing properties are too variable to be used alone as a motor command to drive an external control object via brain-machine interface without averaging over many neurons. Thus, instead of establishing a fine adaptive motor control by using cerebellar neural activities, we developed a cerebellum-machine interface (CMI) to understand cerebellar roles in motor learning, enabling to test direct causality between single cerebellar Purkinje cells and behavioral adaptation in the current study. Our results indicated that single unit vestibulo-cerebellar Purkinje cells are capable of reducing the motion error by adaptively changing their firing pattern. This result is the first direct evidence showing that single vestibulo-cerebellar Purkinje cells in goldfish can be responsible for adaptive motor control. We also found that changes in the Purkinje cell firing patterns did not always reduce, but sometimes increased, the control error, even when significant amounts of error were still present. This perplexing behavior of single Purkinje cells has also been found in monkeys when they were undergoing VOR motor learning [2]. These results suggest that the current theory of cerebellar motor learning postulating Purkinje cell output is adapted to reduce motor error by modifying parallel fiber – Purkinje cell synaptic efficacy requires reconciliation. In addition, we showed that some Purkinje cells can change firing patterns only in their on-

direction, thus they could potentially be responsible for inducing directionally selective VOR motor learning that has been demonstrated to exist in monkey [3] and goldfish [6].

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