



A real-time model of the cerebellar circuitry underlying classical conditioning: A combined simulation and robotics study

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Abstract

Although key components of the cerebellar circuitry relevant to classical conditioning have been identified, the question how they act together is still unresolved. In this simulation study, we investigate a real-time model which captures basic anatomical and physiological properties of this system. We show that this model displays realistic learning performance over a range of inter-stimulus intervals, and demonstrate its stability using a mobile robot solving an obstacle avoidance task. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

In the paradigm of classical conditioning, a distinction is made between components for non-specific and specific learning [5]. The former learning system is characterized by rapid acquisition and physiological and anatomical investigations suggest that it is critically dependent on the amygdala. The specific learning system is characterized by the shaping of discrete skeletal movements to particular task requirements and displays slow acquisition. It is primarily identified with the cerebellum.

We have developed a series of neural models of classical and operant conditioning, called distributed adaptive control (DAC), that we have tested using behaving

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real-world devices [12]. In this approach we hypothesized that the role of the non-specific learning system is to construct a representation of the conditioned stimulus (CS), or stimulus identification, which we have elaborated in neuronal control structures for robots [11,13] and biophysically detailed models [8]. The present project addresses the properties of the complementary specific learning system; the cerebellum.

In this model, we follow the classical view of Marr that learning in the cerebellum is critically dependent on changing the efficacies of the parallel fiber synapses in the cerebellar cortex [6] and that of Albus that learning at this level is expressed by depressing these synapses [1]. In addition, we include the hypothesis of spectral timing which proposes that the ability of cerebellar circuits to represent the time intervals between conditioned and unconditioned stimulus events are due to properties local to parallel fiber synapses [2]. At the level of the overall cerebellar system our model explicitly evaluates the hypothesis that the interaction between Purkinje cells in the cerebellar cortex, the nucleus interpositus anterior, and the inferior olive constitutes the critical circuit which controls and stabilizes cerebellar learning [4]. In this modeling study, we investigate the implications of these assumptions on the functional properties of the cerebellum in classical conditioning.

2. Methods

Fig. 1A depicts the central anatomical elements of the cerebellum incorporated in our model. The CS and US inputs to the cerebellum are provided, respectively, by the Mossy Fibers (MF), originating in the pontine nucleus (Po), and the climbing fibers (CF), which originate in the inferior olive (IO). Mossy fibers make excitatory synapses onto granule cells (Gr), which give rise to the parallel fibers (PF). Parallel fibers, in turn, form excitatory synapses onto the Purkinje cells (Pu) and the basket and stellate interneurons (I) in the cerebellar cortex. The IO gives rise to the US conveying CF which also converge onto the Purkinje cells. Due to this convergence of PF and CF onto the Purkinje cells, these neurons are seen as the site where the memory underlying specific learning is formed [9]. The neuronal precursors of CRs are generated by the nucleus interpositus anterior (NIA) which receives inhibitory projections from the Purkinje cells.

Central to our model is the assumption that Purkinje cells operate in two modes. In the default mode they are spontaneously active and induce a constant level of hyperpolarization in the NIA. In the CS mode the I neurons, which are coactivated by the PFs, suppress the spontaneous activity of the Purkinje cells and the response of the Purkinje cells depends fully on the PF inputs. It is only in this mode that CRs can be generated.

Plasticity of the PF-Purkinje cell synapse can regulate the duration of the Purkinje cell response in the CS mode. We assume that the long term depression (LTD) of this synapse shortens the duration of the Purkinje cell response to the CS, which can lead to a disinhibition of the NIA neurons. In which case the NIA neurons can repolarize and generate rebound spikes, triggering a CR [3]. In our model the PF-Purkinje cell

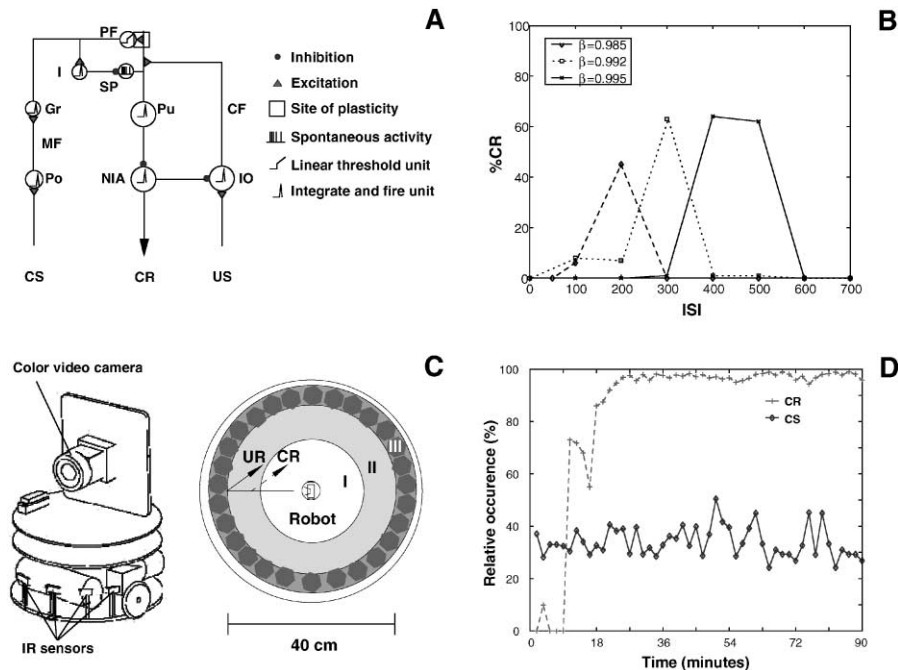


Fig. 1. (A) Basic elements of the modeled cerebellar circuit. See text for explanation. (B) Learning curves of a circuit with varying values of persistence of the PF synapse, β , over several CS-US intervals. β is a multiplicative decay of the membrane potential and indirectly defines the time constant. (C) The microrobot Khepera (left panel) was equipped with a color CCD camera, which was tilted at an angle of 60° towards the horizontal plane. The CS is defined by a population of neurons responding to the presence of red in specific regions of the video image. USs were derived from the infra-red sensors which, in this experiment, signal the presence of IR reflecting surfaces at 1 cm from the sensor. The basic robot control structure and visual processing network are described in Ref. [12]. The US is a rotational movement over about 45° . The avoidance task was performed in a circular arena with a diameter of 40 cm which was constructed with a solid wall of red Duplo blocks. In this arena, three regions can be distinguished. The neutral zone (I) where both CSs and USs cannot be sensed, the CS domain (II) where the camera can sense the red surfaces of the blocks, and the US surface (III) where the IR sensors can be activated due to collisions. (D) Performance of the robot over 90 min expressed by the ratio of CRs over all avoidance actions (dashed). Solid line represents the average responses of the neurons responsive to the CS. Data is averaged over time bins of 100 s.

synapse will only change efficacy when both its pre- and post-synaptic components are active. The polarity of the change, depression or potentiation, depends on the state of the post-synaptic neuron, defined by the integrated excitatory input E^{Pu} . If E^{Pu} exceeds a LTD threshold the synapse can depress, while LTP can occur when E^{Pu} falls in a lower range. When E^{Pu} is in between these two ranges no change will occur. The LTD threshold defines that only values of E^{Pu} induced by coincident activation of the parallel and climbing fibers can depress the synapse [7].

Given this mechanism of plasticity, effective timing of the CR depends on the gradual weakening of the PF-Purkinje cell synapse and subsequent shortening of the

Purkinje cell response and reduction of NIA repolarization latency. Once accurate timing of the CR occurs, the acquired synaptic efficacy is stabilized by inhibition of the IO by the NIA that prevents transmission of US signals to the Purkinje cells [4]. The central parameter which defines the range of CS-US inter stimulus intervals (ISI) over which CRs can be acquired is the duration of the response of the PF-Purkinje cell synapse [2].

Simulations and robot experiments were performed with IQR421 [10]. All neurons are modeled as integrate and fire units with a fixed subtractive afterhyperpolarization. The PF-Pu synapse is modeled as a linear threshold unit.

3. Results

We first investigated the relationship between the duration of the PF-Pu synapse response and the effective ISIs. Three different durations were tested using a conditioning protocol consisting of 10 blocks of nine paired CS-US trials and one CS alone trial each. The learning curves (Fig. 1B) demonstrate that realistic acquisition is displayed over an ISI range of about 100 to 500 time steps where for each condition, a typical Gaussian like learning curve is generated.

In order to investigate whether our model is able to learn to generate CRs under more realistic conditions we incorporated it in a neural control structure for a mobile robot which had to learn to avoid colored obstacles (Fig. 1C). Learning consists of triggering rotational motion (CR) in response to the detection of red patches in the image (CS). Hence, due to learning the robot is able to explore its environment without colliding with the obstacles. The learning curve (Fig. 1D) shows that after about 18 min 80% of the rotational movements were CRs. Learning stabilized at around 95% CRs after about 25 min. This level of performance remained constant over the remaining 65 min of the experiment. The second, solid, curve shows the average amount of activity of the CS cells. It demonstrates that over the whole experiment the robot explored its full environment spending approximately 40% of its time in regions II and III of its arena.

4. Discussion

We have demonstrated that a model, which reflects basic properties of the cerebellum, can acquire and retain CRs where only one parameter, the duration of the PF-Pu synapse response, can control the ISI range where effective acquisition can take place. We have shown that this model can be generalized to an adaptive control structure for a mobile robot. Our results demonstrate that the basic principles captured in our model are robust in a real-world task environment over extended periods of time.

Our model does not provide a complete description of the interactions between the different components of the cerebellar circuitry that are thought to be related to classical conditioning. For instance, it has been shown that both the MF and the CF

form excitatory, and possibly plastic, synapses within the NIA. These connections were not incorporated in the model. We have rather focussed on the cerebellar cortex and its afferent and efferent circuitry in order to explicitly investigate the contribution of the cerebellar cortex, as opposed to the deep nuclei, to normal levels of conditioning. Our model demonstrated that plasticity in the cerebellar cortex can fully support specific learning of the timing of conditioned responses.

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