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The cerebellum: An incomplete multilayer perceptron?

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Abstract

Experimental studies have demonstrated the involvement of the cerebellum in showing classical conditioning paradigms including acquisition, extinction, savings, and spontaneous recovery of the conditioned eyelid response in rabbits. A few experimental studies suggest that the cerebellum is also able to show negative patterning (exclusive or) given that a sufficiently large interval between the conditioned stimulus onset and the unconditioned stimulus onset is provided. In this study, we use a detailed simulation of the cerebellum to shed light on the mechanisms underlying the computation of the *exclusive or* function. The results suggest that the timing of the conditioned response and the computation of the negative patterning paradigm are mutually exclusive.

Keywords: Cerebellum; Granule cells; Eyelid conditioning; Exclusive or

1. Introduction

When an animal receives an unconditional stimulus (US), it generates an unconditional response (UR) based on a reflex. For example, a puff of air sent to the eye will elicit an eyelid closure and a tap on the knee will elicit a leg flexion. If the US is paired with a conditional stimulus (CS) for a sufficient number of times, then the animal learns to produce a conditioned response (CR) even when the CS is presented in the absence of the US. The most widely known example is the experiment conducted by Pavlov [19] in which food (US) was paired with a bell ring (CS) many times until the bell ring alone was able to produce salivation (CR).

Classical conditioning comprises a wide variety of paradigms including negative patterning, also known as exclusive or, which consists of alternating three types of trials by using two conditioned stimuli (e.g. tone and light) and one unconditioned stimulus (e.g. air puff). The first two trials consist of presenting each conditioned stimulus (CS) coupled with the unconditioned stimulus (US) delivered at the CS offset. The third trial consists of presenting both conditioned stimuli and omitting the unconditional stimulus. The animal learns to generate a conditioned response to each conditioned stimulus individually but not to the compound stimulus.

Many experimental studies converge on the important role played by the cerebellum in eyelid conditioning [18,24]. A relatively small number of experimental and theoretical studies [2,7,11,20] bring forward evidence for the ability of the cerebellum to show the negative patterning paradigm. Kehoe [11] has shown that the rabbit cerebellum is able to compute the *exclusive or* function for interstimulus intervals larger than 800 ms. The interstimulus interval (ISI) represents the time between the conditioned stimulus onset and the unconditioned stimulus onset. As the ISI gets longer than 1 s, the timing precision of the CR is reduced drastically suggesting that the timing mechanism used for short ISIs (100–800 ms) is no longer directly involved. These two experimental findings suggest that the timing mechanism needs to be inactive for the cerebellum to compute the exclusive or function.

Theoretical studies [7,20] suggest that the cerebellum should be able to compute the exclusive or function. So far, no detailed simulation of the cerebellum that uses integrate and fire neurons is able to describe how the cerebellum performs the negative patterning paradigm.

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In this study, we use a detailed computational model of the cerebellum [15] to shed light on the mechanism used to compute the exclusive or function. The model is not capable of learning the exclusive or function directly by applying the standard negative patterning paradigm. Our simulations suggest that this failure is due to the timing mechanism which is mainly active in the first 500 ms after stimulus onset. We replaced the standard paradigm with a modified version that eliminates the involvement of the timing mechanism and focuses on making associative connections between the US and an internal representation of each CS. These internal representations in the granule layer contain no temporal dynamics, meaning that they are active only when the corresponding stimulus is on. The internal representation of the compound stimulus is very weak due to the mutual inhibition present in the granule-Golgi layer. Thus, the model learns to respond to individual stimuli but not to the compound stimulus.

2. Computational model of the cerebellum

The anatomy and physiology of the cerebellum has been described in great detail [4]. At a coarse level, the cerebellum receives input through mossy and climbing fibers. Whereas the mossy fibers bring information from the spinal cord and the cerebral cortex, the climbing fibers convey information from the inferior olivary nucleus. The mossy fibers provide information to the cerebellar cortex which includes the granule layer, the Purkinje layer and two layers of interneurons: the Golgi layer and the basket/stellate layer. While the mossy fibers provide input to the granule and Golgi layers, the climbing fibers project directly into the Purkinje layer. The output of the Purkinje layer constitutes the only efferent pathway from the cerebellar cortex. This pathway inhibits the deep nucleus and keeps it from producing a response. At the same time, the output of the deep nucleus, which also constitutes the output of the cerebellum, inhibits the climbing fibers.

Many computational models that capture the main results of classical conditioning have been proposed [6,8,9,16,17,22]. Some of them have architectures based on simplified versions of the cerebellum and some use different architectures altogether. These models propose different explanations for how the cerebellum performs timing. Due to the non-trivial experimental limitations in recording from granule cells [3], none of these models has been validated experimentally.

In this study, we use the detailed model of the cerebellum developed by Mauk and Donegan [13]. As shown in Fig. 1A, the model uses six different cell types, and resembles closely the connectivity ratios between layers. All the details implemented in the model have an empirical basis. While CS is delivered by the activation of the mossy fibers, the US reaches the cerebellum through the climbing fibers. The command for generating the motor action is provided by the output of the deep nucleus [23].

The model contains two sites of heterosynaptic plasticity [5,10]. The synapses at the granule to Purkinje cells undergo plasticity whenever they are activated by the presynaptic granule cell. If the climbing fiber becomes activated 50–150 ms after the activation of the presynaptic granule cell, then the synapse undergoes long-term depression (LTD), otherwise it becomes potentiated.

The synapses at mossy fibers to deep nucleus cells are regulated by the activity of the Purkinje cells. High Purkinje cell activity combined with activity in the mossy fibers produces LTD. A reduction in Purkinje cell activity (e.g. when the cell stops firing) combined with mossy fiber activity produces long-term potentiation (LTP). This particular learning rule has not yet been confirmed experimentally. However, according to Ref. [14] this rule is the only one that agrees with the experimental data.

It has been proposed that the granule-Purkinje synapses store part of the strength of the association between the CS and the US and that the ISI is indirectly stored in the duration it takes each trial to activate the sequence of granule-Purkinje synapses that underwent net LTD during

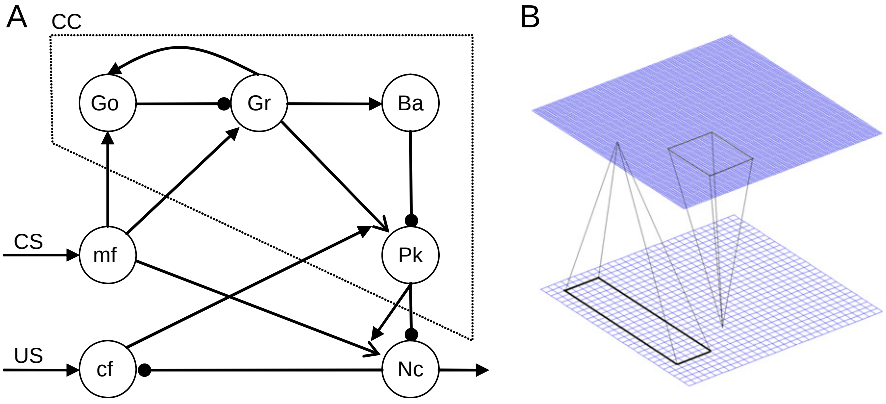

Fig. 1. (A) Diagram of the computational model: cf, climbing fiber (olive cell); mf, mossy fibers; Go, Golgi cells; Gr, granule cells; Ba, basket cells; Pk, Purkinje cells; Nc, nucleus cells; CC, cerebellar cortex; open arrows, plastic synapses; black circles, inhibitory synapses; filled arrows, excitatory synapses. (B) Connectivity in the granule-Golgi system. Upper layer, 10,000 granule cells; lower layer, 900 Golgi cells. The base of the pyramids shows regions from which input cells are randomly chosen to connect to the cell placed at the top of the pyramid.