INTRODUCTION OF NOISE TO THE MODEL OF

CEREBELLAR TRACE CONDITIONING

Eric Culbertson

University of Virginia

ABSTRACT

Trace conditioning is a type of classical conditioning in which a conditioned stimulus (CS) is presented, and then is followed by an unconditioned stimulus (US) after some defined time. Cerebellar eyeblink conditioning is a commonly studied type of trace conditioning in which an animal learns to associate a short tone (the CS) with an air puff (the US). The Cerebellum is sufficient for an organism to achieve learning of this kind and has been modeled previously (**Delianides et al. 2016**). This model was extended to take into account the presence of noise in various components of the cerebellum. Noise was introduced in three critical points: the purkinje cell, the granule cell, and the inferior olive. In response to these changes, the learning time and extinction time was measured.

Introduction

For most animals, simply responding once a threat arises is not good enough to ensure survival. An animal must be able to predict an oncoming threat based on stimuli that are associated with its appearance. For the present study, the threat that the animal must learn to predict is an air puff to the eye. This air puff is painful to the animal, and without receiving some kind of precursor signal, it won't be able to block the puff with a blink. In the study, the air puff is preceded by 300 msec with a short tone. This timing is in line with the Disterhoft trace conditioning paradigm, shown in figure 1 (**Disterhoft 1990**).

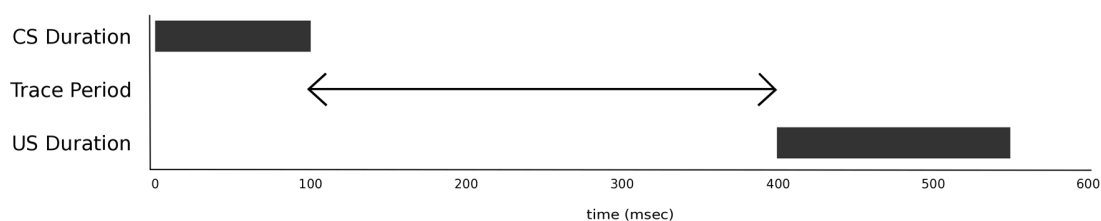Disterhoft 1990 Training Paradigm (Rabbits)

Figure 1: A diagram that shows the trace-conditioning timing outlined by Disterhoft 1990. The tone (CS) last about 100 msec, followed by a 300 msec trace period. After the trace period, the air puff (US) is presented for 150

If the animal learns to associate the air puff (unconditioned stimulus) with the tone (conditioned stimulus), then it will know to blink before the air puff occurs, shielding it from pain. A well-timed blink is known as the conditioned response (CR) within our paradigm. Conversely, failing to block the US with a blink is the unconditioned response (UR).

The Model

The cerebellum has been shown to be sufficient to learning of this kind, so it was chosen to be modeled in this study. Figure 2 shows the relevant underlying circuitry of the cerebellum that was modeled in **Delianides et al. 2016.** This circuitry was based on the work done in the context of delay conditioning (**Thomson 1986)**.
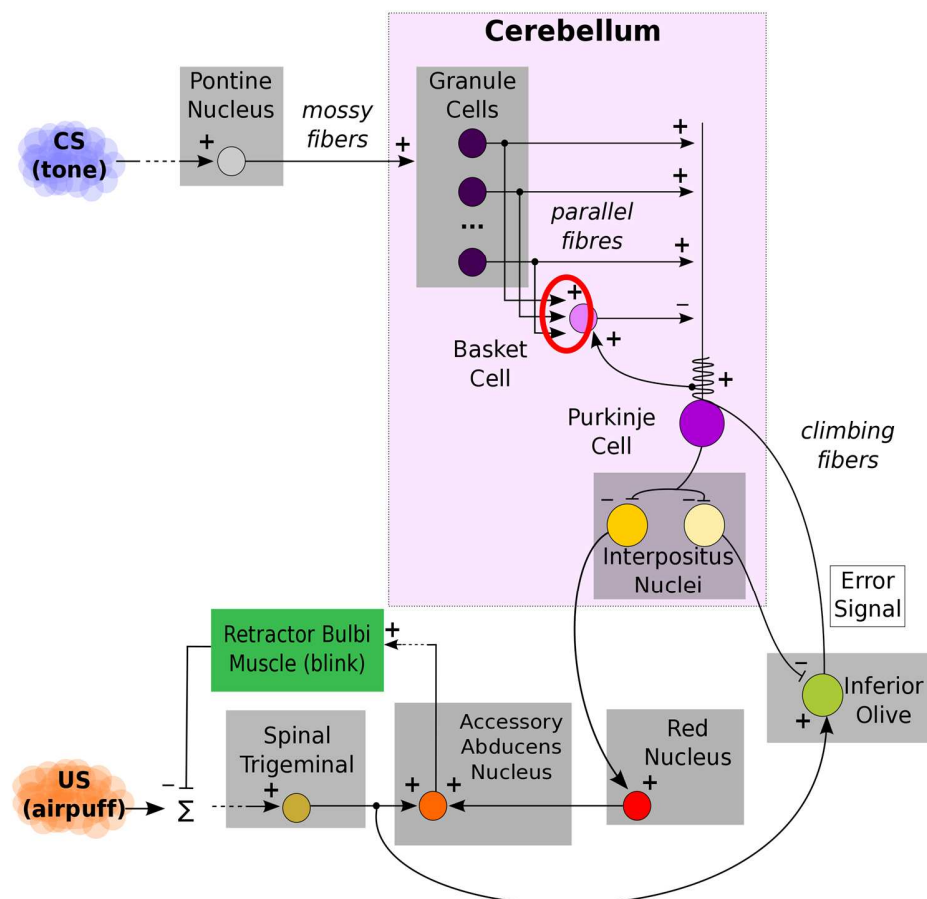

Figure 2: The relevant circuitry behind trace conditioning in the present model. Almost all elements in this diagram are modeled as a single neuron with a firing rate relative to an absolute maximum. The only variable weight belongs to the circled granule cell to basket cell synapse. This is the only site of synaptic modification necessary for learning.

UR Pathway

All the shown components are modeled as a single neuron that fires at some rate relative to its absolute maximum. In order for an organism to blink, the accessory abducens nucleus must fire at a high rate, which in turn causes the retractor bulbi muscle to activate, leading to a blink. As shown in the diagram, the accessory abducens nucleus can be activated from two different pathways. The shorter pathway is caused by the unconditioned stimulus (US). When the airpuff hits the eye of the animal, a pain signal is sent to the spinal trigeminal, which then is activates the accessory abducens nucleus. The other pathway is more involved, and is associated with the conditioned stimulus.

CR Pathway

When a tone is played, it activates the pontine nucleus, which in turn activates the granule cells. The granule cells then send a signal both the purkinje cell and the basket cell. The granule cell activates the purkinje while the basket cell inhibits it. The net effect on the purkinje depends on the weight value of the granule to basket cell synapse. If the purkinje fires at a high rate, it then inhibits the deep cerebellar nuclei (DCN), which prevents a blink. If the basket cell limits the purkinje activity enough however, the CS pathway will lead to a blink. By default, the weight between the granule cells and basket cells is weak. This is beneficial because it ensures that the organism is not wasting energy to blink without reason.

Error Correction

In order to provide the organism with a tool to learn when to blink, an error correction pathway is also present in the model. If the organism did not blink and it

should have, then a positive signal is sent from the spinal trigeminal to the inferior olive. Meanwhile the DCN is constantly sending a negative signal to the inferior olive. After each trial, the net signal to the inferior olive is then sent as an error signal which modifies the weight of the granule cells to basket bells synapse. Without any air puffs, a negative signal is always sent to the inferior olive, which then reduces the synapse weight and decreases the likelihood for a blink. If the organism is consistently getting hit by the air puffs, however, a net positive error signal will be sent, which then increases the likelihood of a blink. Then, once the organism is able to sufficiently block every air puff, the weight of the synapse will stabilize. This system follows that of a classic error corrector **(Rosenblatt 1958; Widrow and Hoff 1960)**. The exact formula is as follows:

$$\Delta w_{GB}(k+1) = w_{GB}(k+1) - w_{GB}(k) = 0.001 \cdot x_g(k, t) \cdot \text{error}(k, t+\Delta)$$

where w_{GB} is the weight of the synapse and x_g is the excitation of the granule cell. With this weight modification, the organism is able to achieve stable learning given enough time steps.

INTRODUCTION OF NOISE

In the study done by **Delianides et al. 2016**, a noiseless system was assumed. However, in all realistic biological systems there is noise of some kind. Therefore, the present study aimed to introduce noise at various areas deemed interesting in a biologically realistic way. Of course, the true nature of noise in a system like this is difficult to determine, so there is no guarantee that the way noise is implemented in this study is biologically accurate. The purpose of this study was to see how noise introduced at various locations in the model could affect learning and extinction. Does

the organism learn faster or slower? Does the organism forget this learned behavior

faster or slower? How is the stable asymptotic equilibrium affected?
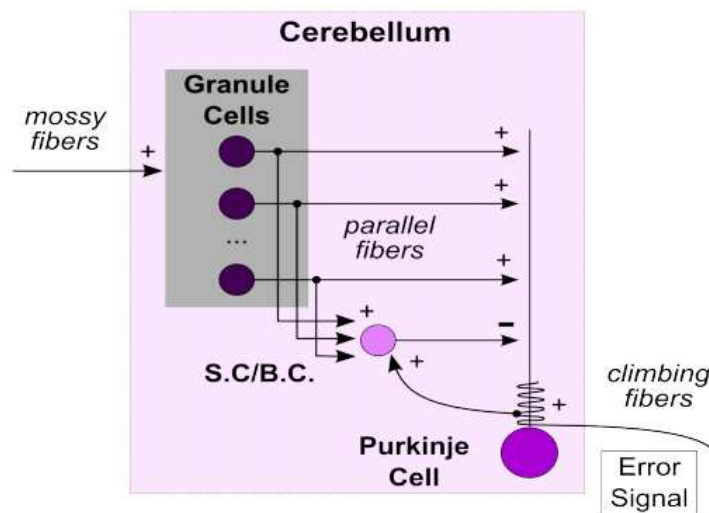
Granule Cell Noise

Figure 3: This diagram shows the granule cells and the components that immediately follow them. If the granule cell is activated by the mossy fibers, it then activates both the purkinje cells and the basket cells.

The granule cells pictured in figure 3, are a critical part of the response pathway. As

implemented in **Delianides et al. 2016**, the granule cell activation is binary. The

activation of the cell corresponds to the presence of a tone 30 msec before. If a tone

was present, the relative activation is set to one, and if no tone was present, the value is

set to 0. To noise up this component, the granule activity was made to be continuous

and random. If a tone was present, the granule cell now samples from a uniform

distribution between .85 and 1, and if no tone was present, then the granule cell

samples from a uniform distribution between 0 and .15. These distributions are shown in
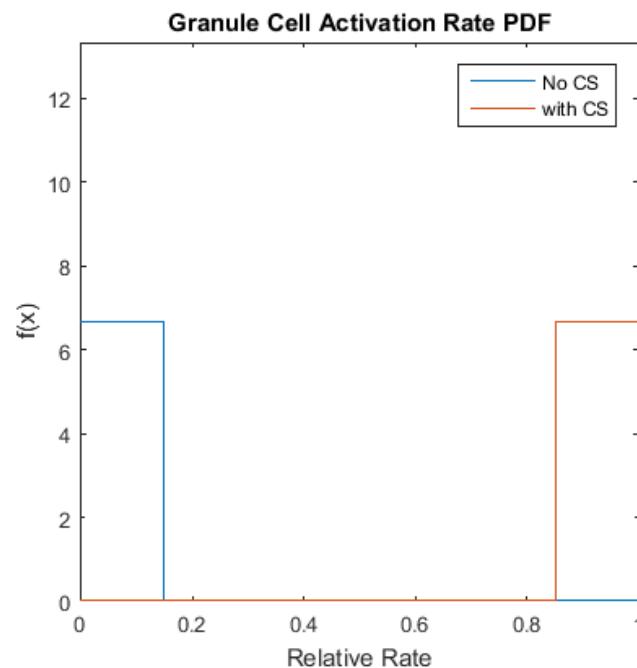
figure 4.

Figure 4: The probability distributions for the granule cell. As shown, the granule cell activity can come from one of the two distributions, depending on the presence of the CS

Because the granule cell directly precedes many other elements in the model, it was predicted that adding variance to the granule cell activity would add variance to all components following it, which are shown in figure 1. This includes the purkinje cell, basket cell, DCN, red nucleus, and the retractor bulbi. Also, in the equation for synaptic modification, the granule cell activity is proportional to change in weight. So a variance in granule cell activity should also influence the magnitude of error correction at each time step. These hypotheses were tested with a series of plots designed to illustrate the process of learning and extinction.

As shown in figure 7 and 8, variance in the granule cell notably gives variance to the motor activity, as well as the activation of the purkinje cell and DCN. Figures 7 and 8 also show that the equilibrium values of activity and granule-BC weight are all much higher than without noise. This is because of the relation between granule cell activity and the granule weight modification. With noise added, the granule cell activity is never zero, so the weight modifications are on average larger with granule cell noise added. This can also be seen in figure 9, which compares performance with and without noise. Adding granule cell noise greatly speeds up learning, because the weight change of the granule to basket cell synapse is on average higher at each timestep. This means that less timesteps are needed for it to reach an appropriately high rate. Also, because its equilibrium rate is so high with granule noise, it takes much longer for extinction to sink in (figures 7vs5, 8vs6, and 9).

Purkinje Cell Noise

The purkinje cell is a critical element behind a properly timed blink. By default, the purkinje inhibits the DCN, which in turn reduces the likelihood of a blink. So in order for the organism to block the US, the purkinje must be inhibited. Adding noise to the purkinje cell should add variance to every element "downstream" from it in the model. This means that noise added to the purkinje will add variance to the DCN, the red nucleus, and to the motor activity. The variance in motor activity should then slow how quickly organism is able to block 100 percent of the air puffs. The organism will need to reach a lower average purkinje rate in order for variance in purkinje activity to not affect the conditioned response.

To test these hypotheses, a random number in the range (-.03, .03) was generated at each time step and added to the purkinje cell activity. This variance added was much smaller than the variance added to the granule cell, because increasing the variance any further completely halts learning. In figures 10 and 11, the variance in purkinje, DCN, and motor activity can be shown. The variance in the motor activity (figure 10) seems to be most affected by purkinje noise. When compared to learning without noise (figures 5 and 6), the equilibriums of the various activities and of the granule to basket cell weight seem largely the same. This seems to suggest that variance in purkinje activity has less effect on learning than the granule cell. This would make sense, sense purkinje activity is not directly used to calculate the synaptic weight modification. In figure 12, the performance over time can be seen. Performance is defined simply as the percentage of air puffs in a session that are blocked. A succesul block was chosen to be when the motor activity is above a value of 0.3. When noise is added to the purkinje cell, it creates a large amount of variability in the motor activity (figure 10). This in turn means that the mean motor activity must be higher to consistence block every puff. That is why in figure 12 shows that it takes longer to reach perfect performance with purkinje noise. This is in line with what was predicted.

Inferior Olive Spike Noise

The inferior olive is the main component responsible for synaptic modification. The nature of its signal determines the sign and magnitude of the weight change in the granule to basket cell synapse. Unlike all other elements in this model, the inferior olive (IO) signal is not modeled as a frequency relative to its absolute max. Instead, it is modeled as a number of spikes in a set time period. According to the research done in

Rasmussen et al. 2013; Najafi and Medina 2013; Mathy et al. 2009, two spikes was chosen to be the point where the error signal is zero. The error signal can then be determined from the spike count ($\#_{t, t+\Delta}$) by the equation

$$\text{error}(\text{k}, t) = \#_{t, t+\Delta} - 2$$

where a negative error corresponds to a decrease in the synapse weight and a positive error will increase the synapse weight.

To add noise to this component, a random amount of spikes was either added or removed from the signal. About 40% of the time, no noise would occur, and there was a 40% chance of adding or subtracting exactly 1 spike, a 10% chance of adding or subtracting 2 spikes, and a 10% chance of adding or subtracting 3 spikes. This noise is likely too exaggerated to be realistic, but was chosen in order to clearly observe its effects on learning. Because spike count has a minimum value of 0 and no maximum value, this noise should have a net positive affect on the error signal. This means that learning will likely be faster and extinction will likely occur more slowly.

Figures 13 and 14 show the learning and extinction process with spike count noise turned on. These plots do not look too different from figures 5 and 6, which show learning and extinction without noise. The equilibrium values are nearly identical with and without spike count noise. The main difference is that the equilibrium lines are slightly less stable. They do not fluctuate nearly as much as with the other types of noise, however. In figure 15, a more subtle difference can be seen. With spike noise, learning is achieved slightly earlier and extinction is achieved slightly later. This is consistent with what was hypothesized, and this effect is likely caused by the noise's net positive effect on the error signal.

DISCUSSION

All sources of noise seemed to affect learning in some noticeable way, but some sources of noise had a more noticeable effect than others. In the cases of the granule cell noise and spike count noise, the learning speed was actually increased the presence of noise and extinction time was decreased. While it is true that fast learning is usually beneficial, the mechanisms that allowed the organism to learn quickly can also lead it to identify false positives. Identifications of false positives is detrimental for an organism because it can waste energy preparing for stimuli that won't actually occur. This is likely why noise is not purely beneficial to an organism, even if certain types can increase learning speed.

To further this study, noise can be added to other components in the model as well. Additionally, noise could be turned on in multiple components at the same time, to see how this affects learning. Because of the looping nature of the model, however, this quickly makes the outcome very difficult to predict and explain. Despite the complications this would present, this would make the model more biologically accurate.
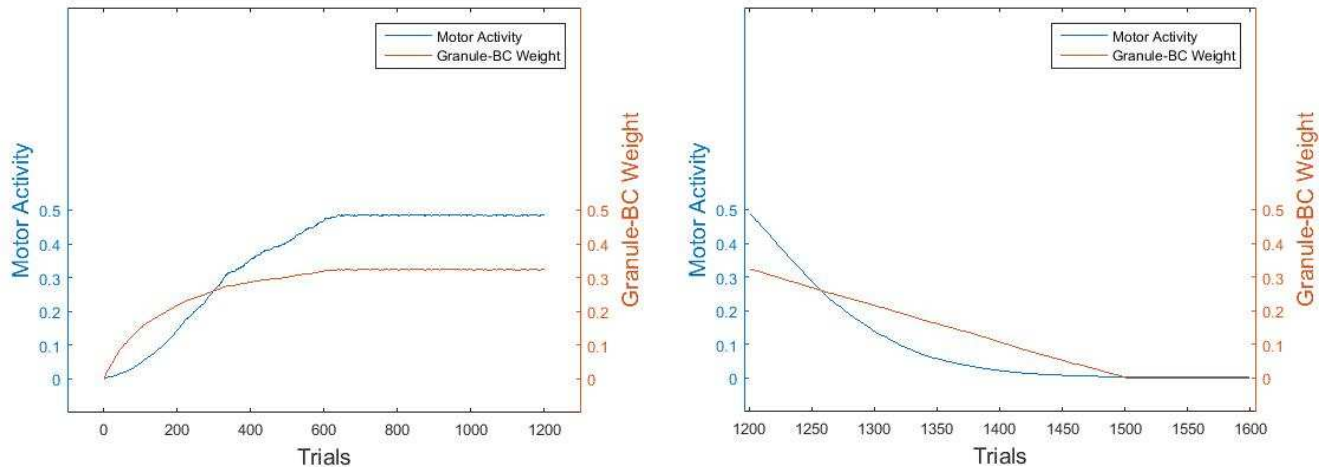
APPENDIX

Figure 5: These two plots show how the motor activity and granule weight evolved during the learning (left plot) and extinction (right plot) periods. No noise was added to the model when these plots were generated. In the learning plot, the lines reach an equilibrium once learning is achieved.
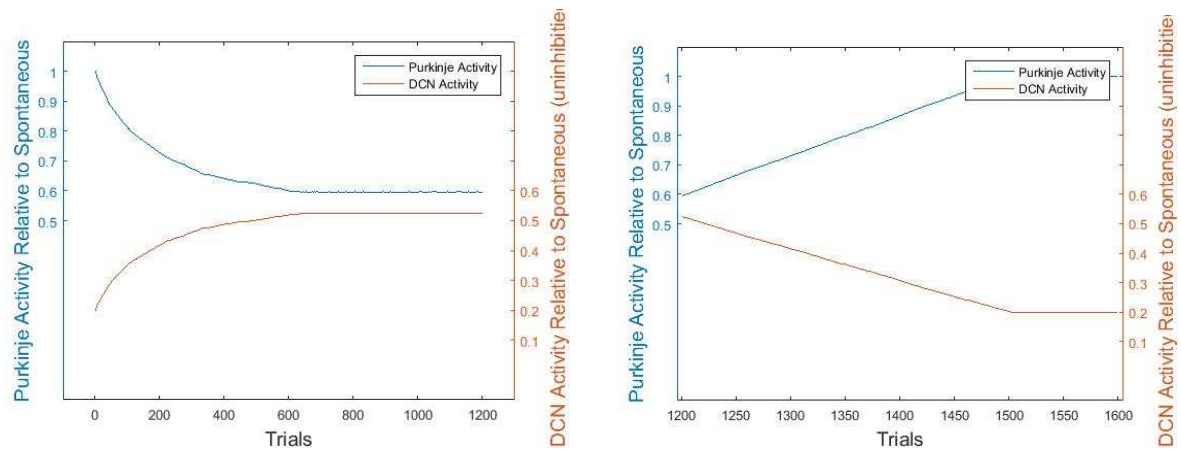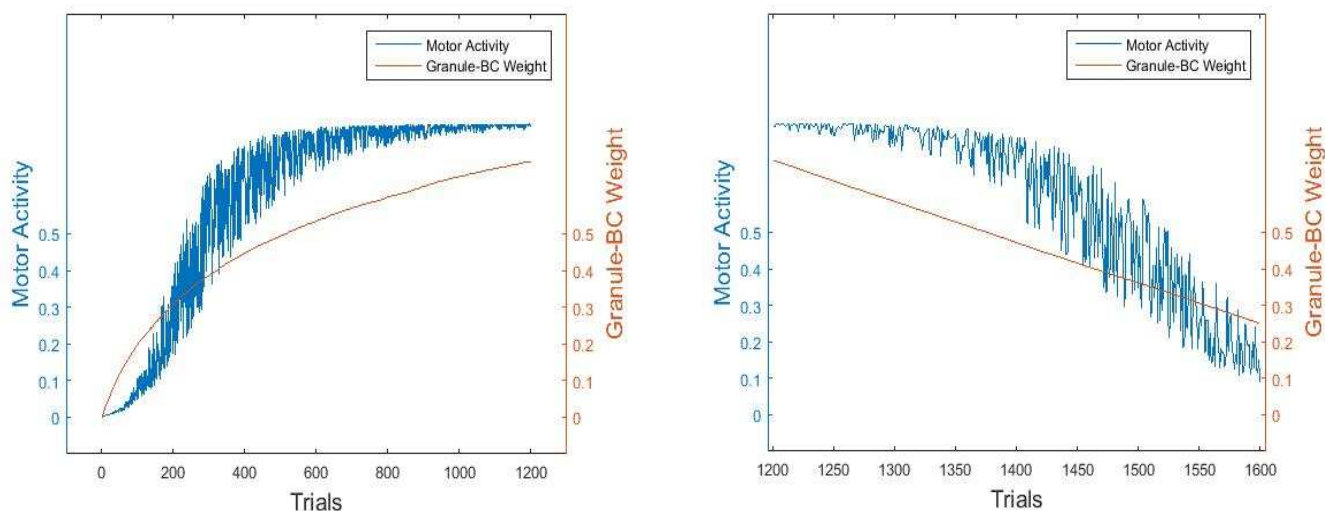

Figure 6: These two plots show how purkinje and DCN activity evolve during learning (left plot) and extinction (right plot) periods. No noise was added to the model when these plots were generated. In the learning plot, the lines reach an equilibrium once learning is achieved.

Figure 7: In these plots, noise was introduced to the granule cell. Just as in figure 5, these two plots show how the motor activity and granule weight evolved during the learning (left plot) and extinction (right plot) periods. The granule weight and motor activity reach a higher rate than without noise, and extinction lasts much longer.
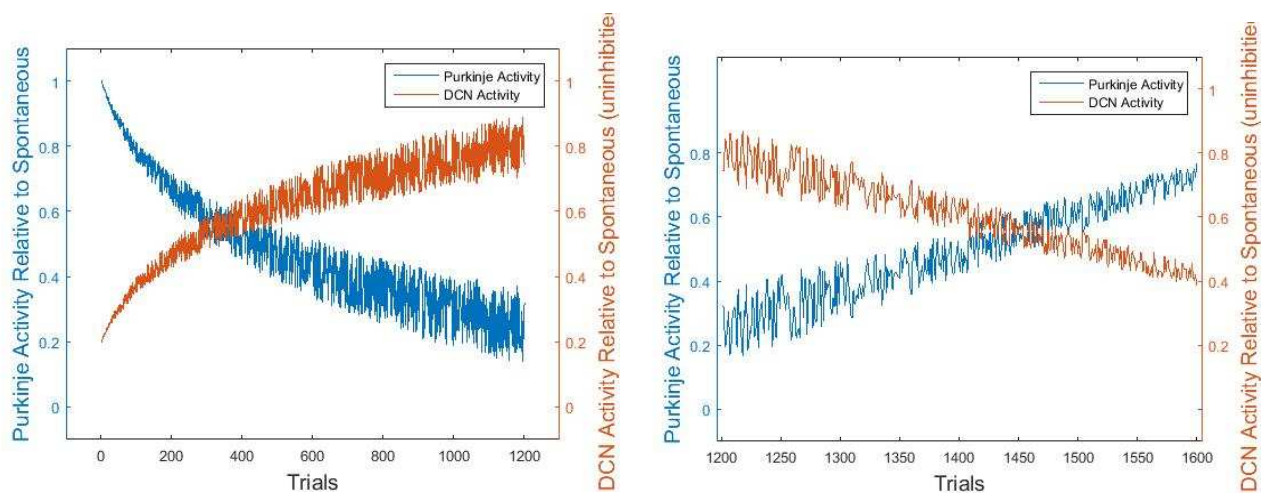

Figure 8: In these plots, noise was introduced to the granule cell. Just as in figure 6, these two plots show how the purkinje and DCN activity evolved during the learning (left plot) and extinction (right plot) periods. The purkinje equilibrium rate is lower with granule noise than without, and the DCN equilibrium rate is higher.
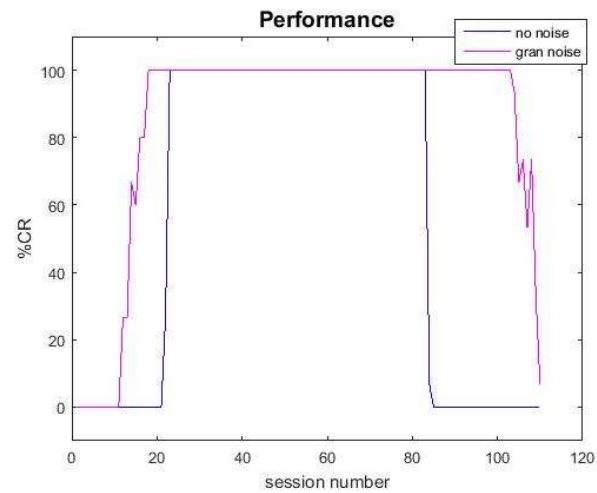
Figure 9: This plot shows the performance of the model with granule noise overlaid with the performance of the model without noise. Performance is defined here to be the percentage of air puffs sufficiently blocked within a session. For an air puff to be sufficiently blocked, the motor activity must be at least 0.3.
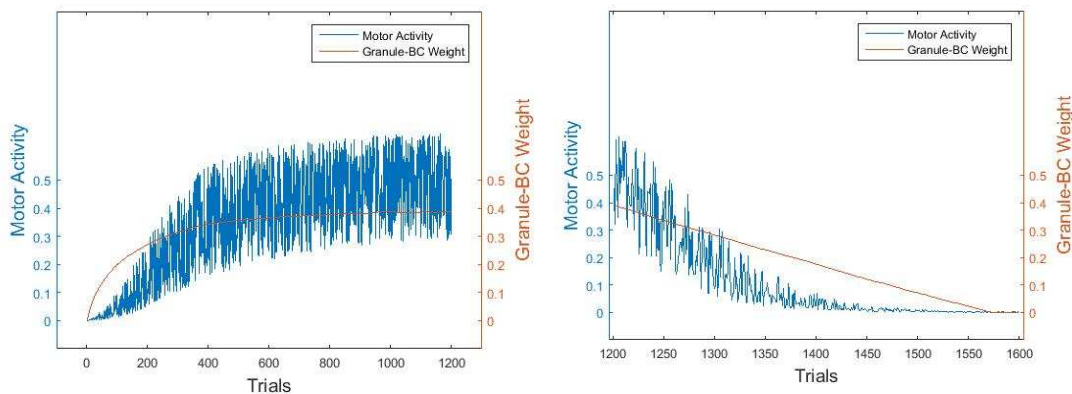

Figure 10: In these plots, noise was introduced to the purkinje cell. Just as in figure 5, these two plots show how the motor activity and granule weight evolved during the learning (left plot) and extinction (right plot) periods. The motor activity is incredibly variable in these plots, despite only a small amount of variability in the purkinje.
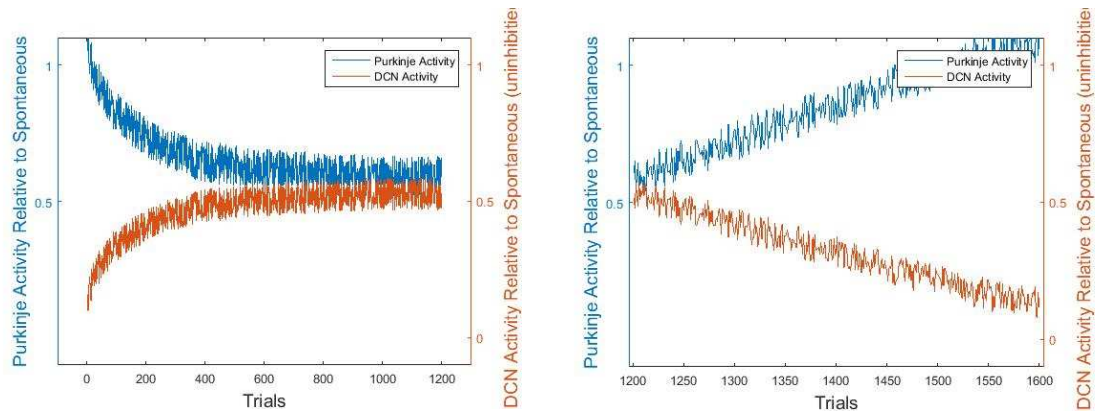
Figure 11: In these plots, noise was introduced to the purkinje cell. Just as in figure 6, these two plots show how the purkinje and DCN activity evolved during the learning (left plot) and extinction (right plot) periods. The purkinje and DCN equilibrium rates are about the same as with no noise, but the rates now have a range of values they fluctuate between.
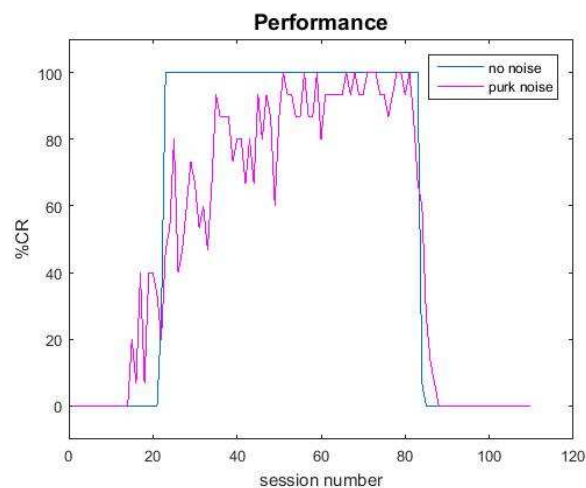

Figure 12: This plot shows the performance of the model with purkinje noise overlaid with the performance of the model without noise. Performance is defined here to be the percentage of air puffs sufficiently blocked within a session. For an air puff to be sufficiently blocked, the motor activity must be at least .3. With purkinje noise, it takes longer to reach 100% performance.
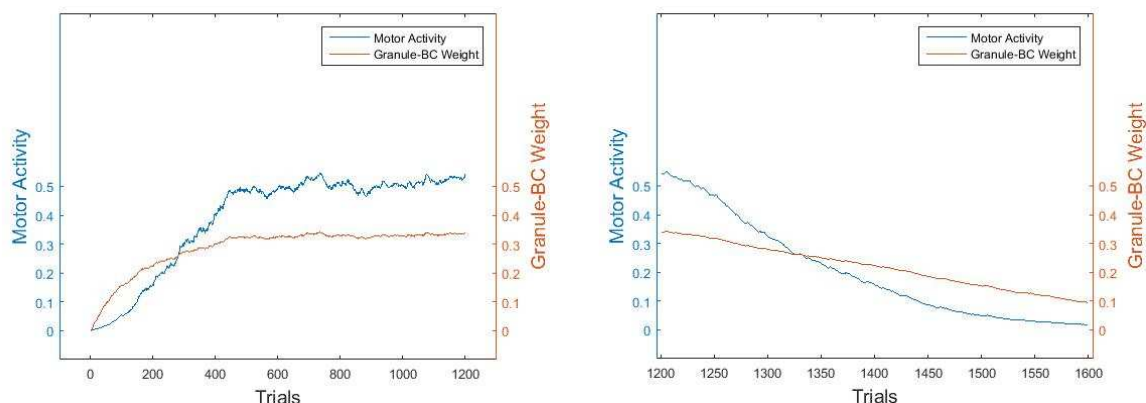
Figure 13: In these plots, noise was added to the inferior olive spike counts. These two plots show how the motor activity and granule weight evolved during the learning (left plot) and extinction (right plot) periods. No noise was added to the model when these plots were generated. In the learning plot, the lines reach an equilibrium once learning is achieved. The equilibrium values reached with noise are about the same as without, but the equilibrium value in the spike noise case is less stable.
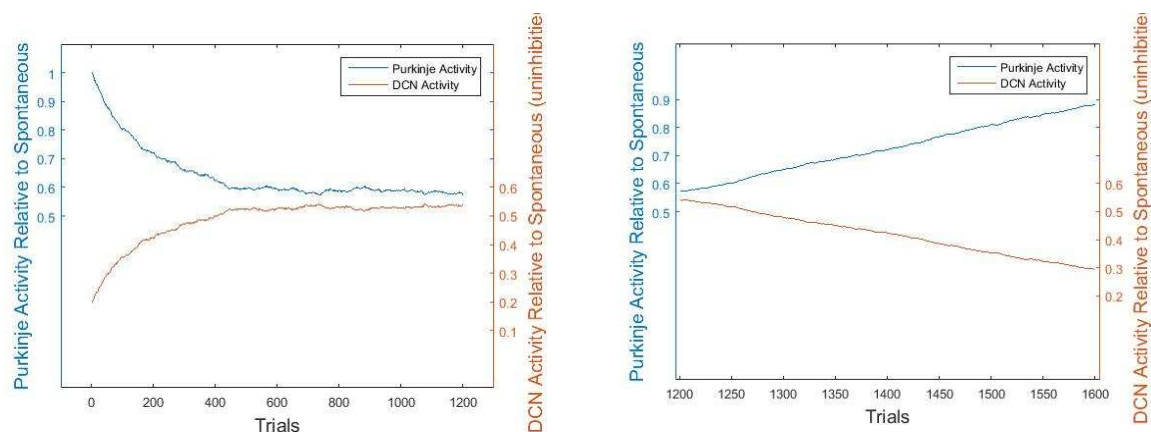

Figure 14: In these plots, noise was introduced to the inferior olive spike counts. Just as in figure 6, these two plots show how the purkinje and DCN activity evolved during the learning (left plot) and extinction (right plot) periods. The purkinje and DCN equilibrium rates are about the same as with no noise, but the rates now are slightly less stable.
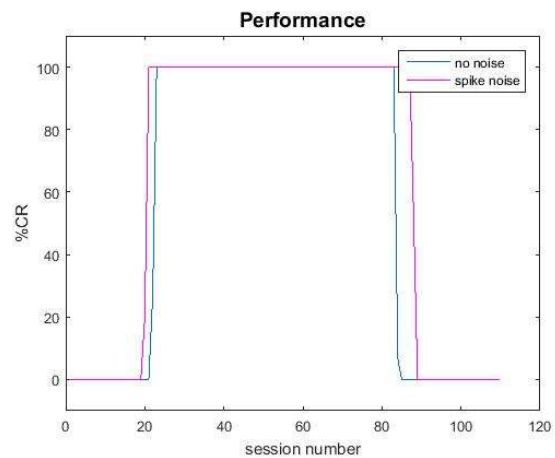
Figure 15: This plot shows the performance of the model with inferior olive spike count noise overlaid with the performance of the model without noise. Performance is defined here to be the percentage of air puffs sufficiently blocked within a session. For an air puff to be sufficiently blocked, the motor activity must be at least .3. With noise added, learning is achieved slightly earlier and extinction happens slightly later.

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