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Experimental and Computational Studies of Cortical Neural Network Properties Through Signal Processing

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Experimental and Computational Studies of
Cortical Neural Network Properties Through Signal Processing

A thesis submitted in partial fulfillment
Of the requirements for the degree of
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by

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Abstract

Previous studies, both theoretical and experimental, of network level dynamics in the cerebral cortex show evidence for a statistical phenomenon called criticality; a phenomenon originally studied in the context of phase transitions in physical systems and that is associated with favorable information processing in the context of the brain. The focus of this thesis is to expand upon past results with new experimentation and modeling to show a relationship between criticality and the ability to detect and discriminate sensory input. A line of theoretical work predicts maximal sensory discrimination as a functional benefit of criticality, which can then be characterized using mutual information between sensory input, visual stimulus, and neural response,. The primary finding of our experiments in the visual cortex in turtles and neuronal network modeling confirms this theoretical prediction. We show that sensory discrimination is maximized when visual cortex operates near criticality. In addition to presenting this primary finding in detail, this thesis will also address our preliminary results on change-point-detection in experimentally measured cortical dynamics.

Acknowledgements

Special thanks to my wife Sarah Withem, my family and the wonderful professors who helped me get to where I am today.

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Introduction

Many physical systems undergo a dramatic change – a phase transition - when the interactions between the parts that make up the system are tuned. Phase transitions can also occur in neural systems (Plenz, 2014). In this context, the collective dynamics of a large network of neurons can shift dramatically when the interactions between neurons are tuned. Criticality is a phenomenon that occurs at a phase transition between two operating regimes. In our study we look to examine criticality within the context of complex neuronal networks in the brain. The brain is made up of approximately 10^{10} neurons with each neuron connecting to tens of thousands of others. As neurons receive information from connected neurons it integrates this input over a short period of time - if the total input is greater than a given threshold the neuron fires. By tuning the strength of interactions among neurons, it is thought that you can tune a neural system through a phase transition. When the interactions are tuned precisely to the tipping point of the phase transitions, the neural system is thought to operate at criticality (Shew, Yang, Yu, Roy, Plenz, 2011). Given that criticality requires finely tuned interactions, it was surprising when experiments found evidence for criticality in real living neural systems both in vivo and in vitro (Beggs, 2003; Thiagarajan, 2009; Fagerholm, 2014).

How could a neural system be tuned to maintain criticality? One way that interactions among neurons are tuned in real brains is through adaptation. Adaptation refers to changes in the synapses mediate neural interactions. Usually adaptation occurs in response to changes in activity or input to the neural system. In theory, adaptation is a possible mechanism that can tune synapses to criticality. (Levina, Herrmann, Geisel, 2007). Why might real neural systems be tuned to operate near criticality? One possible reason comes from studies showing that there are

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functional benefits to being within this critical regime – dynamic range, information transmission and information capacity are all optimized (Shew, Plez, 2012). Similarly, separate studies have shown that adaptation plays a key role in optimizing neural information processing (Kohn, 2007). Putting these ideas together, it stands to reason that adaptation may tune real neural systems to criticality to take advantage of the associated functional benefits. Until recently, there was not experimental evidence to support this idea. However a new study has shown evidence that adaptation to sensory input can tune a neural system to criticality. It was shown that 1.)When driven by an outside stimulus there is transient period where the network is driven out of criticality and 2.) After a period of adaptation the network comes to criticality (Shew et al, 2015).

When the brain is in criticality studies have indicated that stimulus discrimination is maximized – but other aspects of sensory processing, such as stimulus detection, may not be. For instance, studies in which criticality was not considered have shown that adaptation improves discrimination while decreasing the ability to detect small stimulus (Ollerenshaw, 2014). This study was done in the somatosensory cortex of rats. Does a similar tradeoff between discrimination and detection occur in visual cortex? For instance, when a new stimulus appears it would be beneficial to see that it has entered our field of view - detection. Then after we see that a new stimulus is present, adaptation occurs so that we can discriminate the details of the new stimulus and react accordingly.

The work completed for this thesis was designed with two goals. First, we aimed to determine if there was a tradeoff between detection and discrimination. Second was to relate these two functions to the neural network properties, specifically in the context of criticality. We

experimentally tested this hypothesis in the visual cortex of eye-attached whole brain prep of turtles by recording activity in the visual cortex while various stimuli were displayed on the turtle's exposed retinal. We discovered that there was indeed a tradeoff between detection and discrimination. During the onset of the stimulus the neural network exhibited a high detection and low discrimination and in the post transient after adaptation had occurred the network exhibited a high discrimination and low detection. Rather than viewing the critical regime as a binary state, critical or not, we developed data analysis methods to assess the 'proximity to criticality' that will be described in the methods section. The results show a distinct relationship between proximity to criticality and response to stimulus.   Near criticality, discrimination was high and detection was low. Far from criticality, the opposite trend was found; discrimination was low and detection was high.

Experimental Procedure

Our experimental procedure involved taking extracellular voltage readings from visual cortical brain tissue of attached-eye ex vivo experiments in turtles. Voltages were recorded using a Neuronexus microelectrode array with 128 electrodes arranged in a three dimensional 4x4x8 grid. The electrode array was inserted to depths in the cortex of approximately 700-500 µm. This array was used in conjunction with the Blackrock Microsystems neural recording suite. This equipment was used to observe and record the local field potential (30 kHz sample rate, band-pass filtered between 5-100 Hz) of the visual cortex. The electrode had to be modified to fit our needs and our system limitations. The electrode connectors were modified using standard soldering techniques to limit our usage to the bottom 96 electrodes, and not connecting to the highest section of 32 electrodes. This essentially changed the layout to an active 4x4x6 grid of active electrodes. This was beneficial to the brain prep as it allowed constant flow from our

perforation system over the cortex, ensuring it had access to proper nutrients and oxygen. To perform the experiments on the visual cortex of the turtle with the electrode arrays the turtle brain was prepared in an eye-attached whole brain preparation (Saha D, Morton D, Ariel M, Wessel R, 2011). Once the brain had been removed from the skull the dorsal cortex was surgically unfurled from the DVR to reveal the visual cortex. The time between the surgery was kept short (~1 min) and the brain was immediately moved into the recording chamber onto a soft agar block and submerged in a saline solution. The recording chamber was constructed with a perfusion system to keep the room temperature saline oxygenated. The brain was perfused with oxygenated saline at all times during the experiment. The brain was given a rest time of thirty minutes to an hour following surgery to allow anesthetic drugs to leave the system. Once the brain was prepared the microelectrode array was placed into the cortex using a microcontroller and a microscopic webcam to ensure precision and proper placement. The method for electrode placement was to move the electrode with the microcontroller to slightly above the exposed visual cortex and then moved down in 50 um steps with a rest time of five minutes between each step. During this rest time a live feed of electrical spiking of the neuronal network could be seen. When there was a majority spiking response throughout the active portion of the electrode array the stepping process ended and we allowed the electrodes to settle for 15 minutes before beginning the visual stimulation and data collection. A graphic of the microelectrode placement can be seen below as well as photos from the microscopic webcam:
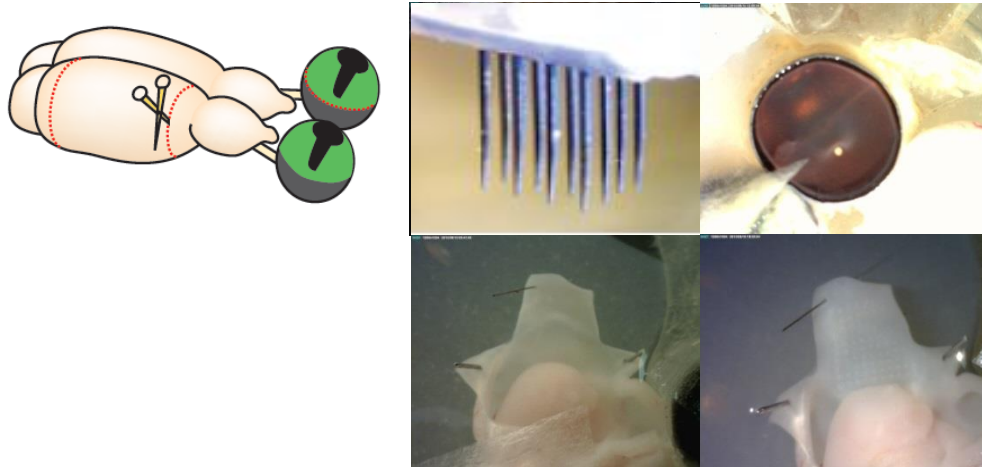
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Figure 1 – (Left) After removing the brain with eyes attached from the turtle, three cuts (red dashed lines) are made to facilitate the unfolding of the cortex and remove the lens exposing the retina in one eye. Approximately half of the 96 electrodes are located in visual cortex. (Right, Top Left) Photo of microelectrode array used in neural recordings. (Right, Top Right) Photo of retina post-surgery in the remaining half of eye. (Right, Bottom Left) Photo of the uncurled section of the visual cortex. The bulb centered below the pinned flap is the DVR. (Right, Bottom Right) Photo of the uncurled section of the visual cortex post experimentation. Note the small imprint left by the microelectrode array.

The visual stimuli were focused directly onto the exposed retina of the turtle. The full experimental setup can be seen below:
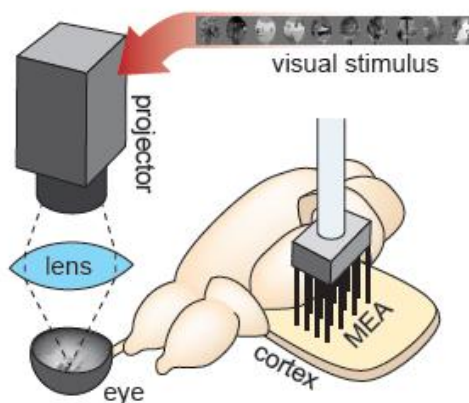

Figure 2 – After placement of the electrode as seen in Figure 1, a lens is placed above the exposed retina that allows for the visual stimulus that was projected from a digital projector to be directly focused onto the retina so that it receives the entire stimulus. The 96 channel microelectrode array (MEA) was used to measure how the network of neurons in visual cortex responds to the visual stimulation of the retina.

The stimulus paradigm was designed to allow us to measure both detection and discrimination of visual stimuli. The detection of a visual stimulus will be assessed based on neural response to what I will call the background stimulus. The discrimination will be assessed based on the neural response to a foreground stimulus that plays on top of the background stimulus. The background stimulus will be either a gray screen or a movie (Nishimoto, Gallant, 2011). The stimulus that was projected onto the retina was a group of four different types of stimulations. The 4 types can be seen below in Figure 3. Each type of stimulation was played for five seconds with thirty seconds of black screen in between. First, a movie would be played with a red dot projected within 0.3 seconds of the movie being turned on – this represents a stimulus being presented during the transient of the stimulus onset Second, a gray screen would be shown with a red dot presented four seconds after the stimulus onset – this represents a stimulus being presented after adaptation had occurred. Third, a movie would be played again with a red dot at four seconds and finally, a gray screen would be played with a red dot at the transient. Both the movie and the grey screen were modified to have the same overall contrast and intensity. To test whether our main conclusions generalize across different background stimuli, a shuffled version of the movie was also used. The red dots varied in intensity from 1 (grey dot) to an intensity of 4 (very bright red dot) for each set of four stimulations. A total of twenty complete sets were shown for each recording taken.
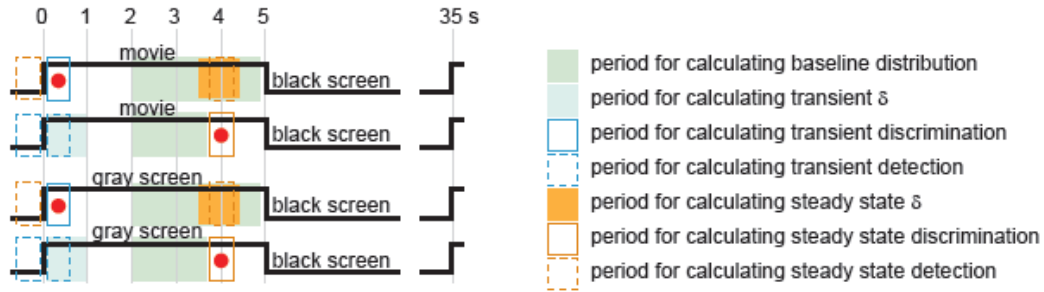
Figure 3 – Timing diagrams for the four different types of stimulation sets presented to the retina and definitions of the transient and steady state periods.

For each stimulus set a synchronous signal was sent from the stimulus set computer to the neural recording device to mark the beginning of each break and start of new stimulus, regardless of set. For each turtle the stimulus sets were performed while the turtle was submerged in a saline bath. Full experimentation was run on a total of 12 turtles for this study.

Data Analysis

The goals of the data analysis are as follows:

1. We compared transient versus steady state visually driven neural activity. This allows us to assess changes in how neural networks operate as the system adapts. The transient response is interpreted as the response before adaptation has occurred. The steady state response differs from the transient response due to adaptation.

2. Make avalanche distributions that will be used to assess the 'closeness to criticality' measure that will be called δ for the remainder of the paper. Criticality appears in neural networks due to the dynamical synapses that govern them and one key feature of this criticality is the presence of power law observables (i.e. Neuronal avalanches) (Levina, Herrmann, Geisel, 2007).

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3. Compute the discrimination capabilities of the visual cortex via the visual stimulation system described in the experimental methods section.

4. Compute the detection capabilities of the visual cortex using the visual stimulation system.

5. Compare how both detection and discrimination depend on this 'closeness to criticality', δ.

The data that was recorded from the Blackrock Microsystems recording suite was unfiltered and had a noise of less than 10 µV. For post recording data analysis the data was passed through a Butterworth bandpass filter from 5 Hz to 100 Hz to examine the low-frequency components as well as a Butterworth notch filter from 59 Hz to 61 Hz to remove electrical noise. This low frequency band is referred to as local field potential (LFP) in neuroscience research. Large amplitude fluctuations in LFP occur when many neurons are active together. In all of the following results, we study LFP-based neural activity.

We first define a *LFP peak* (black dots in Figure Xb) using an event threshold defined at two standard deviations. Peaks that occurred either beneath the negative threshold or above the positive threshold were considered LFP peaks. An avalanche is defined as a spatiotemporal cluster of LFP peaks with inter-peak intervals $< \Delta T$. The size of an avalanche is defined as the number of peaks within a given avalanche. We examined distributions of avalanche sizes to assess how close the system was to criticality. A graphic showing the characterization can be seen below (Figure X, b):
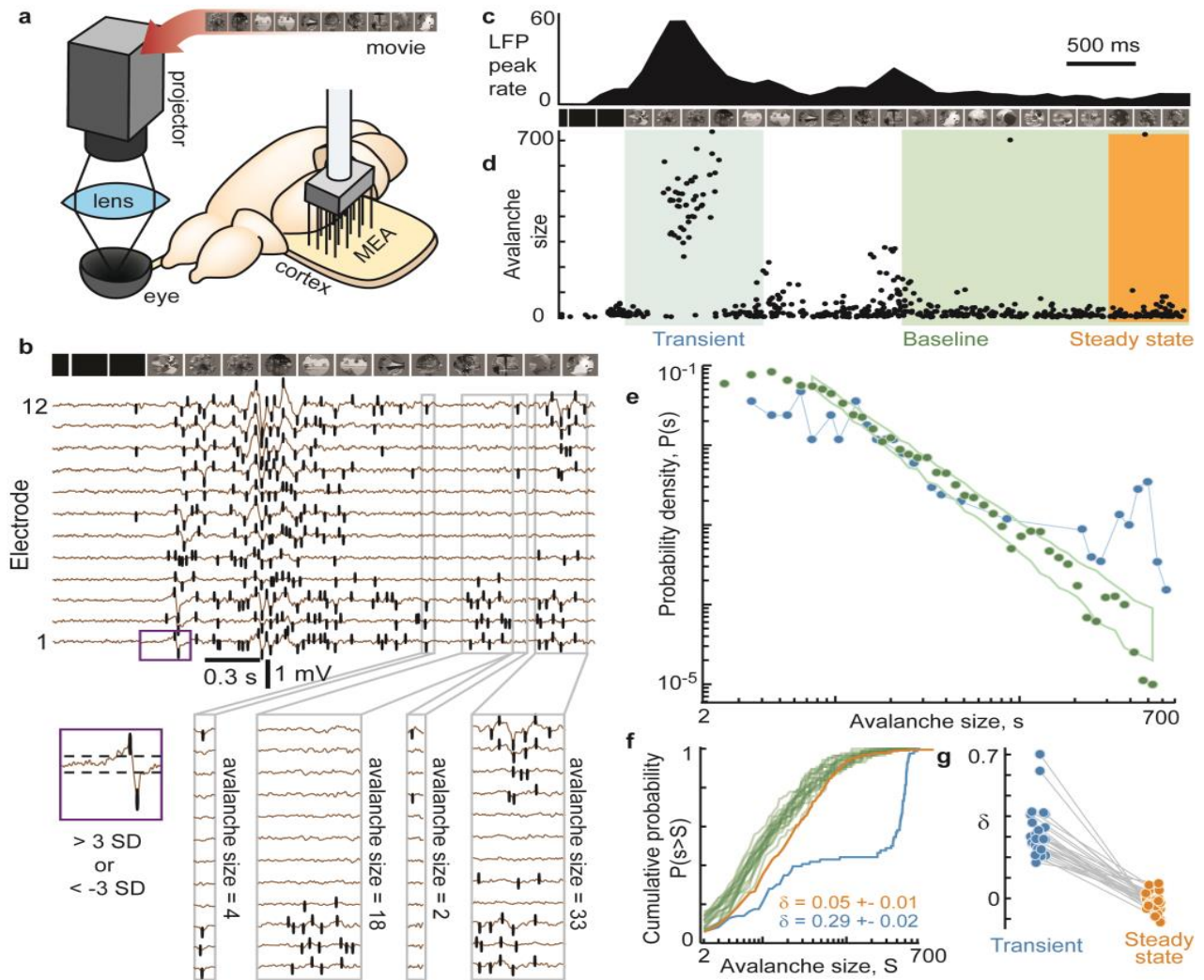
Figure 4 – a.) A diagram showing the experimental setup b.) A sample LFP data during a visual stimulus c.) Averaged LFP rate from all n = 12 samples d.) Avalanche sizes for all n = 12 samples with highlighted areas for transients, baselines, and steady state times e.) An example of probablity density functions of the baseline and transient areas f.) Cumlative distribution function of the transient, baseline and steady state times for one experimental run. The multiple baseline graphs represent the 20 random subsample draws g.) Graph showing the δ of transient and steady state areas with slight random spread for readability

To compare the transient and steady state visually driven responses we first examined the

avalanche distributions during each time period. During the transient period the average LFP

peak rate was much higher than that of the steady state period. Later in this section we use

change-point detection to detect the onset of visual response based on the LFP peak rate. We

compared the distributions to a period during the visual stimulus we call the baseline to compute δ. A baseline group of avalanches was defined as those avalanches that occurred during a time period of 2 seconds to 4.5 seconds following the onset the visual stimulus. Avalanches that occurred during times when the foreground red dot stimulus was presented were not included. To obtain a distribution for the transient period we examine a time period of 0 seconds to 2 seconds at the beginning of the visual stimulus. Again, this distribution excluded avalanches that occurred when a red dot was presented during the transient. To obtain a distribution for the steady state period we examined the avalanches from 3 seconds to 5 seconds of the visual stimulus in which no red dot was presented during the steady state. All of these time periods are illustrated in Figure 3.

As found in previous work, we first confirmed that the steady state avalanche distribution was a power-law, which indicates that the system operates near criticality in the steady state regime. Thus our baseline distribution is a power law. We then compared both transient and steady state distributions to our baseline distribution using an n-to-n sample matching with random draws from the baseline distribution twenty separate times. δ is computed by subtracting common points along the log space of the cumulative distributions of transient or steady state from the baseline distribution   The results can be seen in Figure X, showing that during the steady state period, the neural network had a much smaller δ meaning that it was closer to a power law and therefore closer to the critical regime than that of the transient distributions.

The next step was to compare our δ values to how well the system can detect and discriminate visual stimuli. To examine the detection and discrimination of the visual cortex during our visual stimulus we analyzed LFP peaks. We calculated mutual information between stimulus and

response, which response defined in terms of a LFP peak count. To determine the mutual information of a given stimulus we must define what a stimulus is and what a response in terms of our experimentation. We defined a response to a stimulus as the number of LFP peaks within 0.3 seconds of the stimulus rounded down to the nearest ten. The rounding ensures that we have a discrete number of responses for the calculations, and helps mitigate finite sampling bias. The stimulus is defined differently for detection and discrimination. For detection, the stimulus is the transition from no visual stimulus (blackness) to the background movie or grey screen coming on – and therefore a binary stimulus, off or on. For discrimination the stimuli are the red dots that are displayed on top of the background stimulus. These red dots vary between intensities defined generally as intensity levels one, two, three, and four where level one is a grey dot and level four is a bright red dot. Once stimulus and response are defined mutual information can be calculated using MATLAB code (Peng, 2007). After the mutual information is calculated in this way, the data used for calculation is then shuffled and a 'shuffled' mutual information is calculated. This is then subtracted from the original mutual information to avoid finite sampling bias. Both discrimination and detection were computed during the transient period and during the steady state period.

Next we compared the mutual information of detection and discrimination to the characteristic δ. Since δ is a measure of deviation from criticality, we can then answer the question: Are discrimination and detection maximized at criticality or not? We examined the mutual information of the transient avalanches alongside the δ computed using the transient data and the mutual information of the steady state avalanches to that of the steady state δ. The results of this analysis can be seen below in the Results section of the paper.

For the main results reported in the next section the transient period was defined to be the 2 second interval following the onset of the background stimulus, as discussed above. This choice of the transient period duration was based on examining the data by eye, but was somewhat arbitrarily chosen. A more principled method for determining the transient period was also examined. To have a more analytical answer to where the transient truly ends change point detection was used. Change point detection describes a wide array of techniques to determine when the statistics of a group of data changes from one distribution to another. The most basic of these techniques involves knowing both distributions the data set should vary between. In the case of experimental systems the exact statistical distributions vary from run to run and turtle to turtle but the hypothesis was that trends were similar across all experiments. A more advanced method of change point detection, relative density ratio estimation is a non-parametric way of determining when a statistical system goes through a drastic change – i.e. when a visual stimulus is presented (Liu, et al, 2013). Using Liu's paper and attached MATLAB code for the *RuLSIF* process, the neural network activity was examined at the beginning of each visual stimulus. The 2 seconds prior to the visual stimulus playing and the 2 seconds after the stimulus had been delivered and there was no transient dot shown were examined. The number of avalanches was calculated along a sliding window of 0.002 seconds across the total 4 seconds. This data was then used in the MATLAB code from Liu to produce graphs indicating the change point score for the 4 seconds of neural activity. Results can be seen in the Results section of the paper and discussed further in the Future Work section.

Results

As stated earlier in the Data Analysis section, our main goals were to 1.) Examine neuronal network activity during the transient and steady state periods of the visual stimulus, 2.) Compute

a 'closeness to criticality', δ, 3.) Compute the detection and discrimination capabilities of the neuronal network in the transient and steady state periods and 4.) Demonstrate a relationship between detection/discrimination to δ. Our hypothesis was that adaptation plays a key role in this tradeoff between detection and discrimination. If we examine the results of the described data analysis we can make a few observations. The first is that there are relatively few avalanches during the rest periods between visual stimuli when there is nothing shown to the cortex and the eye is in complete darkness. There is a large response to the visual stimulus being shown to the cortex, both grey screen and movie characterized by an increase in the LFP peak rate and drastically increased avalanche size. The cumulative distribution that is produced using these avalanches shows deviations from a baseline cumulative distribution, notably the decrease of smaller avalanches due to the increased amount of very large avalanches. The δ that is calculated during the transient periods through all of the experimentation is much larger than that of the baseline ($\delta = 0$). Although this behavior was typical of most experiments, there were two outliers with significantly higher δ. Steady state neural activity on the other hand was much closer to our baseline with a δ much closer to 0. It can be seen that our baseline produces power-law distributions similar to those of neural systems that are known to be critical. For examples of this see Figure X in the Experimental Methods section.

The data collected during the dot presentations offer insight into the detection and discrimination trade off. We see that there is a strong response to the visual stimulus being shown – so much so that the level of red dot is unrecognizable during the transient period. If we however examine the response to the red dots that are shown during the steady state period there is a marked increase in avalanche size that reflects the increases in intensity of the dot shown. When comparing the

mutual information calculated during these times back to δ, interesting trends appear. In the case of detection, all turtle recordings showed a marked in decrease in detection from the transient period to the steady state period. In the case of discrimination, all but one turtle showed an increase in discrimination between transient and steady state periods.
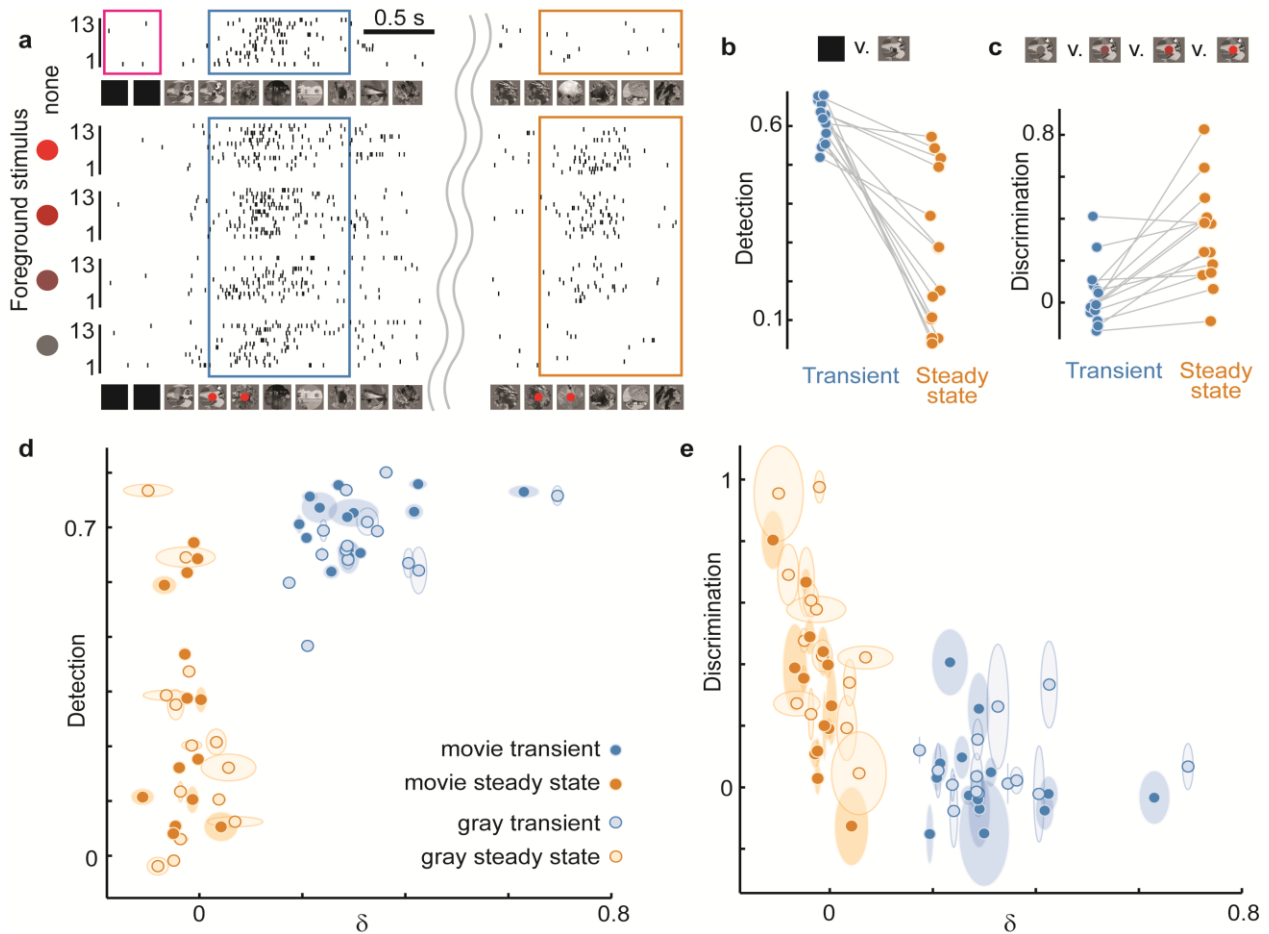

Figure 5 - Adaptation enhances discrimination at the cost of reduced detection. a) Typical raster of LFP peaks (taken from all electrodes, randomly subsampled to 10%) showing response to 52 trials with the same background visual stimulus. A different red dot foreground stimulus was presented during each of four blocks with 13 trials each. The red dot was presented either during the transient period just after background stimulus onset (blue box) or later during the steady-state (orange box). Note that the different foreground stimuli were more easily distinguished by the LFP peaks in the steady-state compared with the transient, but the presence of the background stimulus is more easily detected based on strong transient response. b) Summary (n=14 turtles) of how well the LFP peak count can

detect the presence of the background stimulus. All turtles show a decrease in detection from transient to steady-state. c) Summary of how well the LFP peak count can discriminate the four different foreground stimuli. All except one turtle showed an increase in discrimination from transient to steady-state. d,e) A more refined explanation of detection and discrimination is obtained by comparing to δ. Generally, lower δ resulted in enhanced discrimination and poorer detection, while higher δ exhibited the opposite trend. Thus, power-law distributed (low δ) population dynamics are associated with a functional trade-off, gaining discrimination at the cost of decreased detection.

During the transient period the mutual information was significantly higher for the case of detection than that of discrimination. The steady state period was opposite – with significantly lower mutual information for the case of detection than that of discrimination. Generally we see a trend of power-law distributed (low δ) neural network dynamics are associated with high discrimination and low detection. In contrast, when δ is high (system is far from criticality), low discrimination and high detection were observed. Thus we confirm the existence of the functional trade-off discussed in the introduction – our findings suggest that enhanced discrimination comes at the cost of diminished detection.

Conclusion

Previous studies have shown that within the visual cortex, neuronal activity was pushed away from criticality during a transient period after the stimulus was presented and adaptation was returned the neuronal network to criticality. This study sought to experimentally examine two potential functional benefits of criticality - detection and discrimination of sensory input. We found that there was a tradeoff between detection and discrimination related to a measure of 'closeness to criticality', δ. When δ is low, there exists a functional tradeoff where the network gains higher discrimination at the cost of decreased detection. Our work provides the first experimental for functional advantages of criticality in an intact visual system. Moreover, our

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findings are the first to point out that criticality is not only associated with functional advantages (good discrimination), but can also incur functional disadvantages (poor detection.)

Future Work

In previous work on criticality in the visual cortex of turtles, a neuronal network model was built to theoretically reinforce what was experimentally shown (Shew, 2015). The network model presented in that paper was used in this study as well in an attempt theoretically show similar results and to show that short term synaptic depression (a form of adaptation) was sufficient to explain the tradeoff between detection and discrimination. The network used was an all-to-all connected neuronal network with an n= 1000 neurons. To simulate the visual stimulus used in the experimentation the synaptic input was increased to mimic the background stimulus being played and then increased again for a short period of time to mimic a red dot of varying intensities. In the future, the model will be used to show the discrimination and detection capabilities of a theoretical neuronal network with synaptic depression being the only form of adaptation available.

We were able to obtain strong preliminary results for detecting when the transient period began and ended through the change point methods described in the Data Analysis section. In the future these same methods will be used to categories the time series for transient and steady state areas within the visual stimulus to ensure accurate analysis of these areas.

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