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Adaptation maintains cortical visual processing at criticality

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Adaptation maintains cortical visual processing at criticality

An Undergraduate Honors College Thesis

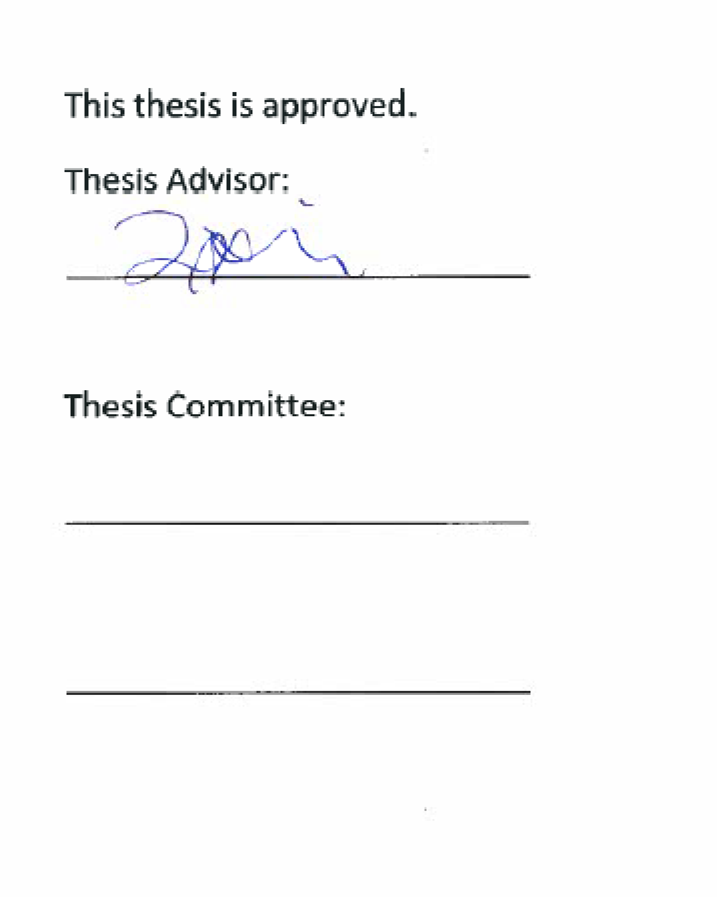
in the

Department of Electrical Engineering

College of Engineering
University of Arkansas
Fayetteville, AR

By

Wesley Patrick Clawson



This thesis is approved.

Thesis Advisor:

Thesis Committee:

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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 paper is on the role of criticality in visual sensory information processing. One line of previous work suggests that the dynamic range of the network, when presented with outside stimulus, is maximized at criticality. Another line of previous work suggests that adaptation to changes in visual input serves to improve dynamic range. A third line of work suggests that adaptation can bring about criticality. Taken together, these three previous ideas suggest that adaptation to visual input will bring about criticality. Thus, our hypothesis was that visually driven activity does operate near criticality, except during a transient period of adaptation immediately after the onset of the stimulus. We experimentally confirmed this hypothesis; we demonstrate that sensory driven cortex dynamics maintain signatures of criticality and in good agreement with our model; the transient response to the stimulus onset is not critical, but supercritical.

Introduction

Self-organized criticality is a key subject that describes complex naturalistic systems (Bak, P., Tang, C. & Wisenfeld, 1987). Our study will focus on the network dynamics of the visual cortex in the brain, specifically in in-tact visual systems of turtles, and how these large networks process sensory information. This in-tact system includes the brain and the two eyes that connect to the brain via the optic nerve. We used work done by others, most notably Heiss, Levina, Adibi, Shew and their respective collaborators in the field of neural networks, self-organized criticality, information processing and neural adaptation to form our hypothesis. Adaptation is a phenomenon observed in almost every sensory system. For instance, you have experienced adaptation whenever you've walked from a dark room into a well-lit area; the short span of time that it takes your eyes and brain to adjust to the vast difference in lighting is a form of adaptation. The specific hypothesis of this study is that adaptation serves to bring neural networks (and therefore visual systems) back to criticality.

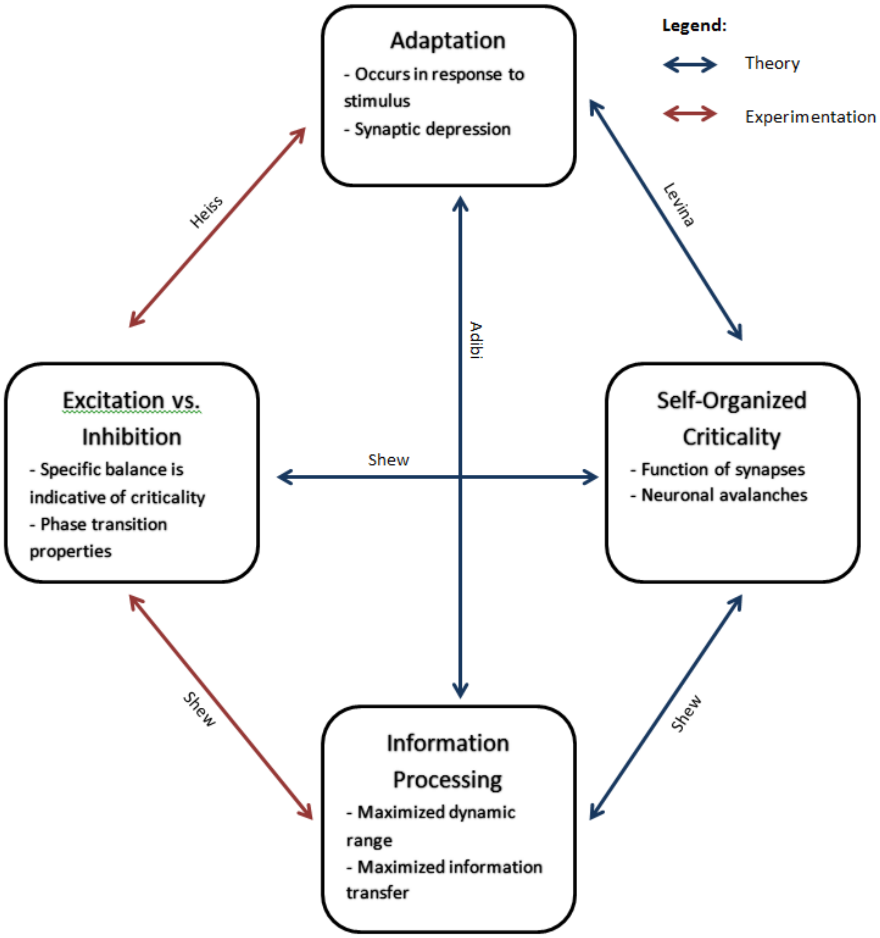

Figure 1 – This graph represents the culmination of the work that we have based our hypothesis on. The lower three fields have been connected to one another by Shew and others. The idea that we aim to bring into the understanding of neural networks is adaptation. As the graph shows Heiss, Adibi, Levina and their collaborators all have contributed to each of these three different fields individually and our experiments show that these four fields can be cohesively brought together.

To better connect the ideas presented, Figure 1 has been included to show the connection between the four different fields and how we used these ideas to form a hypothesis about the visual cortex. Criticality has been hypothesized as a function of balance between two types of neurons that are present in the brain, inhibitory and excitatory. 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 either fires its own action that is either excitatory or inhibitory. The balance of this dynamical system is thought to play a key role in criticality, even being described as one method in which you can tune a neural system into, and out of, criticality (Shew, Yang, Yu, Roy, Plenz, 2011). It was theorized that this self-organized criticality also demonstrated critical avalanches, a type of spontaneous activity in the superficial layers of the cortex both *in vivo* and *in vitro*, and was later experimentally shown (Eurich, C.W., Herrmann and M. & Ernst, 2002); Beggs, Plenz, 2003 and 2004; Plenz, D. & Thiagarajan, T.C 2007). Self-organized 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). Within this framework of excitation and inhibition, criticality can be defined a dynamical regime balanced between two distinct extremes that are bounded as a phase transition (Levina, Herrmann, Geisel, 2009). The first extreme is characterized by highly ordered, intense activity that tends to cascade across the entire network due to over excitation and the second extreme is characterized by disordered, weak activity that does not propagate across the network well due to over inhibition (Shew, Plenz, 2012). These studies show that neural networks operate near criticality during spontaneous ongoing activity (i.e. activity that occurs with no sensory input) but there has been no experimental evidence to whether or not they operate near criticality during activity driven by sensory input.

It has been theorized that adaptation serves as a method to maintain a particular balance between excitation and inhibition; more specifically that inhibition adapts more than excitation (Heiss, Katz, Ganmore, Lampl, 2008). Adaptation also serves to enhance information transmission (Adibi, Clifford, Arabzadeh, 2013) while criticality has the same functional benefit of enhancing information transmission (Shew, Yang, Petermann, Roy, Plenz, 2011). Another key computational benefit of criticality includes maximized dynamic range (Kinouchi, Copelli, 2006; Shew, Yang, Petermann, Roy, Plenz, 2009; Shew, Plenz, 2012). Our hypothesis then follows from this previous work indicating (4) characteristics of neural networks: (1) that criticality has many functional benefits during activity with no sensory input , (2) criticality has been related to the balance between excitation and inhibition similar to phase transitions, (3) adaptation serves to modify the balance of excitation and inhibition in response to outside stimulus, (4) adaptation, similar to criticality, has functional benefits that are associated with it. We hypothesized that the neural network should exhibit criticality during stimulus driven activity, except for a small transient period of adaptation in which the activity is supercritical.

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 our experimentation supported our hypothesis – the network displayed key characteristics of a critical network (i.e. power law distributed neuronal avalanches) during both non-stimulus driven and stimulus driven activity. However the system was found to not be critical during the transient response after the initial onset of the stimulus but rather it was found to be supercritical.

Experimental Procedure

Our experimental procedure involved taking extracellular voltage readings from visual cortical brain tissue of attached-eye experiments in vivo from turtles. To do this we used a ten by ten Utah microelectrode array at depths in the cortex of approximately 500 μm. This array was used in conjunction with the 30Ks/s Blackrock Microsystems neural recording suite. This equipment was used to observe and record the local field potential (5-100 Hz) of the visual cortex. To perform the experiments on the visual cortex of the turtle with the Utah 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. 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. A graphic of the microelectrode placement can be seen below as well as photos from the microscopic webcam:

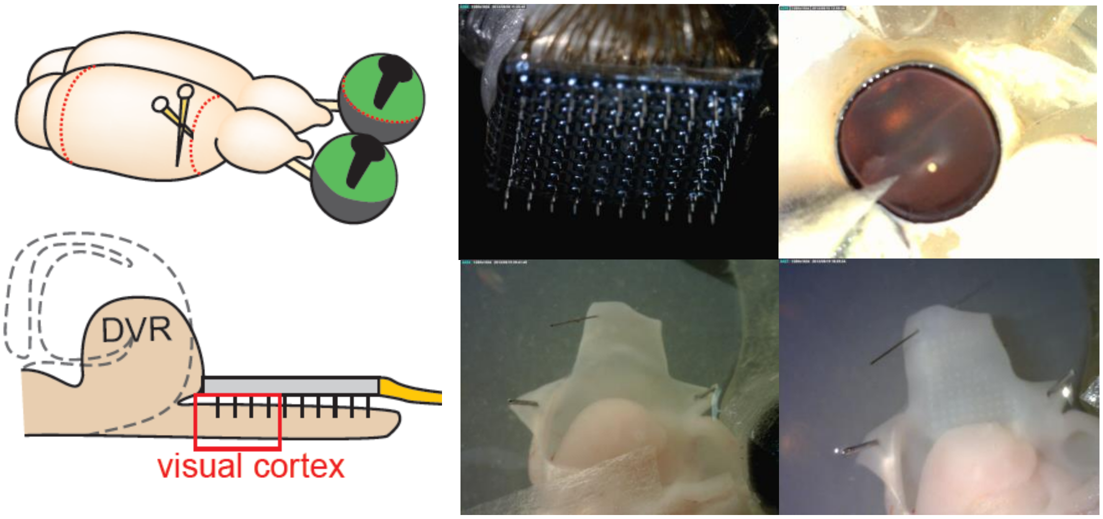

Figure 2 – (Left) After removing the brain with eyes attached from the turtle, three cuts (red dashed lines) are made to facilitate the unfolding of the cortex and remove the lens exposing the retina in one eye. (Bottom) The cortex is unfolded and flattened to allow insertion of the electrode array. 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:

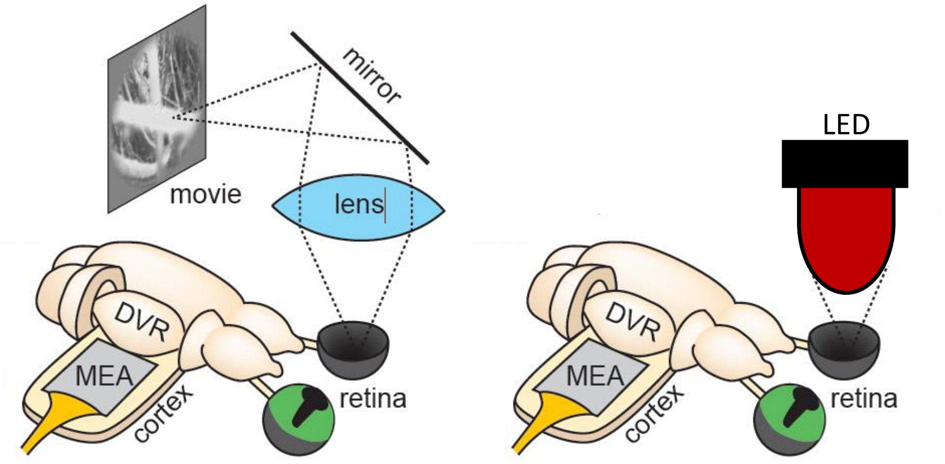

Figure 3 – (Left) After placement of the electrode as seen in Figure 1, a lens is placed above the exposed retina that allows for the visual stimulus that was projected from a computer monitor and reflected from a positional mirror to be directly focused onto the retina so that it receives the entire stimulus. (Right) A 5 mm red LED is positioned slightly above the exposed retina such that when voltage is sent to it the majority of the produced light is shown onto the retina.

We performed three different types of visual testing for the turtles. Our first visual stimulus was a video clip comprised of 10 sec clip from a video recorded with a camera mounted to the head of a cat while it moved through a forest and a 10 s clip from the popular Disney movie, Tarzan. It was normalized in terms of contrast and color. This clip is regarded as a naturalistic movie and has been used in previous studies of the visual cortex (Betsch BY, Einhäuser W, Körding KP, König P (2004)). The first stimulus set, using naturalistic movies, consisted of 15 minutes of naturalistic stimulus, 15 minutes of no stimulus, and 15 minutes of stimulus etc. for 4 hours. The second stimulus used scanning black dots that moved across a white screen in a specific pattern based upon angles of movement. Eight black dots move across the screen for each angle 0, 90, 180, and 270 across a white background. Each of these dots takes two seconds to traverse the screen. A 10 second pause with no motion separates each consecutive dot scan for a total time for one angle of 86 seconds. After each dot set no stimulus is shown for 214 seconds and is then followed by another angle set. For angles 45, 135, 225, and 315, 15 black dots move across a white background. Each of these dots takes 2.83 seconds to traverse the screen with a 10 s pause with no motion to separate consecutive dot scans. The total time for one of these angle sets is 182.5 seconds. After each dot set no stimulus is shown for 117.5 seconds and then followed by the next angle set. This stimulus set was performed for four hours per turtle. The third type of stimulus set was diffuse flashes of a red (5 mm) LED. This stimulus set consisted of a diffuse flash of the LED followed by 119 seconds of no stimulus for a total of 120 seconds, or two minutes. This set was performed 120 times for a total of four hours of recording per turtle. Lastly, spontaneous ongoing activity was also recorded for four hours as a control for each turtle.

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 eight turtles for this study.

Data Analysis

To extract avalanches from LFP data the data was first filtered through a band-pass Butterworth filter to eliminate low (<5 Hz) and high (> 100 Hz) frequencies. To define a neuronal event (black dots in Figure 3) an event threshold was defined at six standard deviations and the peaks that occurred either beneath or above the threshold were considered events. It is important to note that for data consisting of only spontaneous ongoing activity the standard deviation was found by calculating it according to the entire data set. For data consisting of both spontaneous and evoked activity two separate standard deviations were found, one for both type of data set and their respective averages were used to find events within each data set. Next we determined which electrodes were located in visual cortex based on whether they exhibited strong response to visual stimulus. A strong response was defined based on the average response over many repetitions of the stimulus, as shown in the next figure.

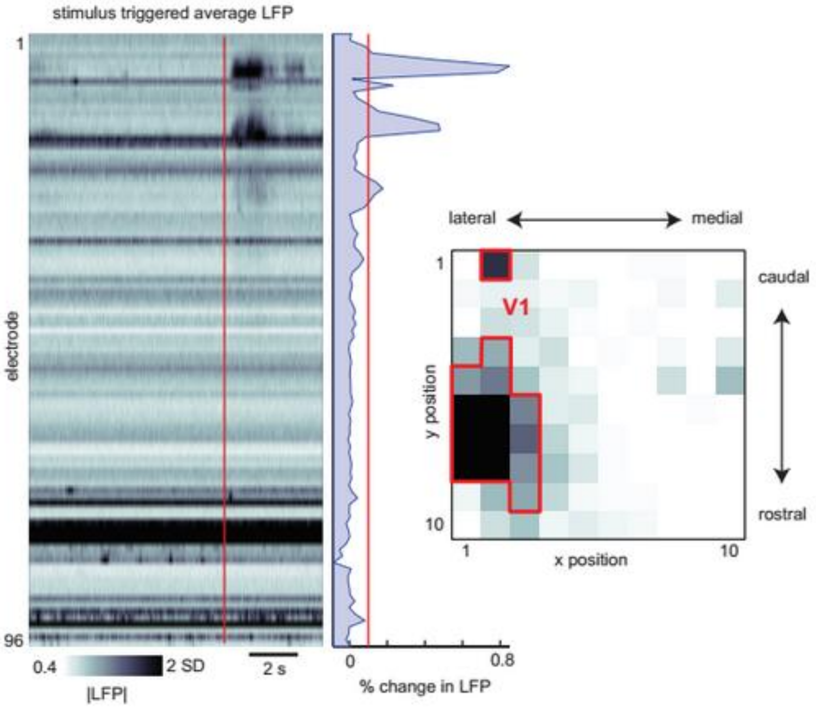

Figure 4 – Graphical representation of the visual cortex during recording sessions. On the left is a graphical representation of the temporal activity to due stimulus for all 96 electrodes. Note that in the lower fourth of the 96 electrodes there was erroneous data on some electrodes, thus the large appearance of activity where there was none. The red bar represents when a stimulus was shown to the exposed retina. In the middle a graph of percent change in LFP fluctuations across all electrodes. The red bar in this graph is a threshold applied to determine which electrodes, and thus which area of the cortex, were active during a stimulus set. The graph on the right is an over the top view of the electrodes looking down during a stimulus set. The area highlighted in red represents the electrodes with active neuronal activity. This area, we call V1, was the area of most activity during stimulus and ongoing activity for all turtles during all stimulus sets. It is on this area that we perform our analysis of transient and steady-state data present later.

An avalanche is defined as a spatiotemporal cluster of LFP peaks, or events, with inter-peak intervals < ΔT. The size of an avalanche is defined as the number of peaks within a given avalanche and the duration is the time between the first and last peak. Using these definitions the neural recording data was categorized to examine criticality. A graphic showing the characterization can be seen below:

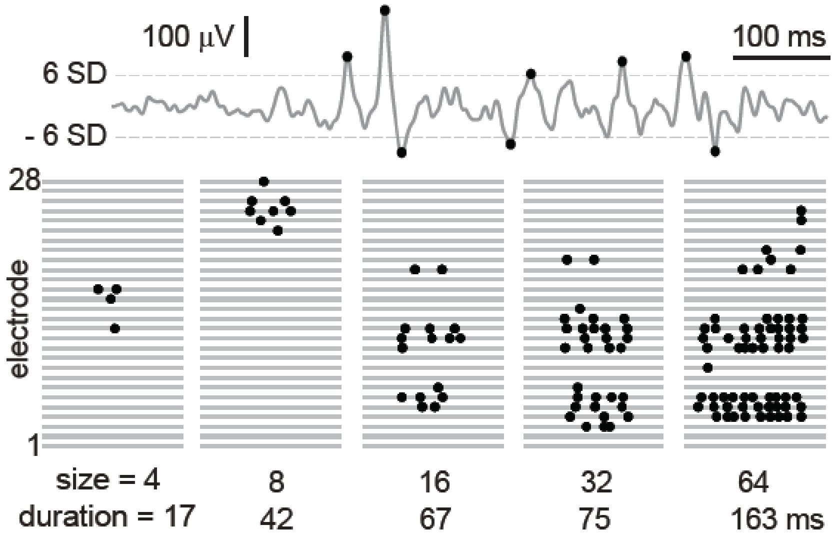

Figure 5 – (Top) An example section of neuronal activity on a single electrode with black dots placed on the peaks of activity that are greater than or less that 6 SD. Note that there may be peaks in activity but not be considered part of an avalanche due to being within 6 SD. (Bottom) Five examples of neuronal avalanches across a sample size of 28 electrodes of the 96 total. Note that these avalanches are spatiotemporally correlated and that as size increases duration does as well.

To examine whether or not the neuronal avalanches had observables that were power law distributed size and duration distributions were made from the now categorized sets of avalanches. These were made by plotting logarithmically both the size and duration of an avalanche against the probability of getting a size or duration greater than that avalanche in two plots. These distributions are called complementary cumulative probability distributions.

Since avalanche size and duration distributions are expected to be power-laws at criticality, we assessed "proximity to criticality" by the following two steps. First we computed the best-fit power-law function to our observed distribution using established maximum likelihood methods (Clauset A, Shalizi CR, Newman MEJ, 2009). Second, we computed how far the observed distribution deviated from the best-fit power-law using the Kolmogorov-Smirnov statistic. This deviation from the best-fit power-law (presented in Figure 9) can be interpreted as a quantitative estimate of deviation from criticality. The larger the deviation, the greater the deviation from criticality. This analysis was carried out for the avalanches that occurred during a short time following the stimulus turning on, i.e.

transient avalanches. It was also carried out for the visually evoked avalanches following the transient and for ongoing activity.

Although power-law avalanche size and duration distributions are one important piece of evidence for criticality, they do not definitively prove that the system is critical. An additional type of evidence comes from examining the relationship between size and duration (show in Fig 8). Theory of criticality predicts that size should increase with duration in a specific way (Friedman N, Ito S, Brinkman B, et al., 2012), depending on the exponents found in the power-laws for size and duration distributions. We also tested how well this prediction fit our observed data (results shown in the inset in Figure 9). The greater the deviation from the prediction, the further from criticality the system is likely to be.

Experimental Results

The data recorded using the Blackrock Microsystems Neural Suite was multi-site ongoing and visually evoked low frequency potentials (LFPs). An example of the data can be seen below:

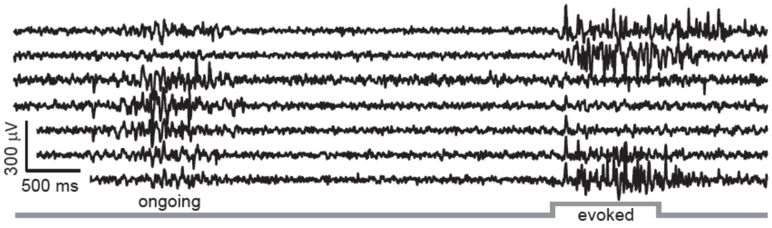

Figure 6 – An example neural recording that shows both ongoing activity and evoked activity across 7 electrodes. The grey bar beneath the data represents the signal sent from the stimulus computer indicating stimulus onset. The ongoing activity is an example of a neuronal avalanche and is characterized by a growth of activity, a peak, and a declination of activity. The evoked activity is characterized by a sharp increase in activity due to stimulus, slight declination and then a steady-state response until the stimulus ends in which the activity declines back to a baseline.

As it can be seen the ongoing and evoked data are both spatially and temporally correlated. The evoked avalanches begin with a large immediate response which lasts ~5 ms, called the transient, which is marked with a large LFP at the stimulus onset. It is these transients that will be discussed in the 'Discussion of Results' section that follows. To ensure that the recorded data was reliable a trial-averaged spatial patterns of the evoked LFPs was calculated and can be seen below:

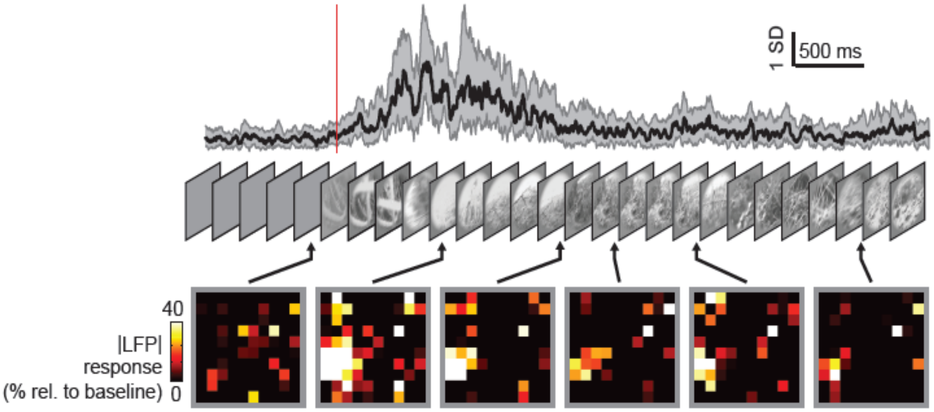

Figure 7 - Top: Black line is the average over 45 repetitions of the movie stimulus. The gray band delineates lower to upper quartiles for variation around the average line.
Middle: Movie images
Bottom: Average spatial patterns of LFP activity at the times indicated by the black arrows. Color indicates % change compared to a baseline period before the movie turns on.

There was also a reliable trial-to-trial low frequency LFP response with respect to general response to stimulus set. This can be seen below:

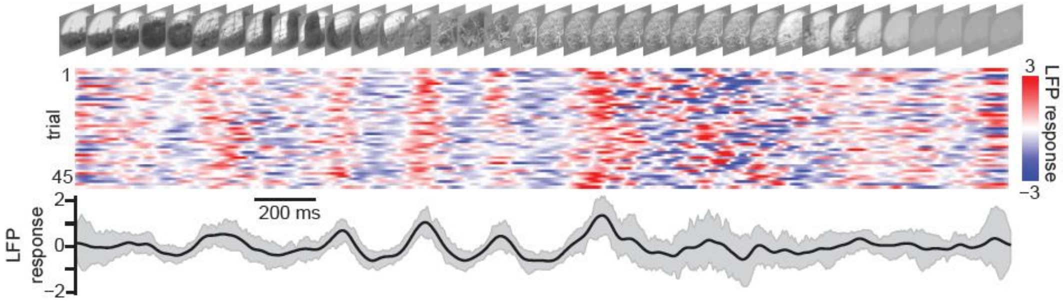

Figure 8 – Top: Scenes from the naturalistic movie
Middle: 45 repeated trials of naturalistic movie as seen by one electrode. This graph is meant to show a reliable response in the visual cortex to the visual stimulus
Bottom: Black line is the average over 45 repetitions of the movie stimulus. The gray band delineates lower to upper quartiles for variation around the average line.

It should also be noted that these results are applicable to all stimulus sets: naturalistic movie, scanning dots and LED flashes.

The focus of this study was the transient responses to visual stimulus and therefore we focused a secondary avalanche characterization, mentioned in the Data Analysis section, on the transient response. In a graph below the pre-stimulus ongoing activity (black), the transient response (red) and the stimulus driven activity (blue) is shown temporally in two ways: avalanche size and avalanche duration. The grey bar beneath the graph represents the pulse sent by the stimulus computer indicating that a stimulus had been sent to the screen.

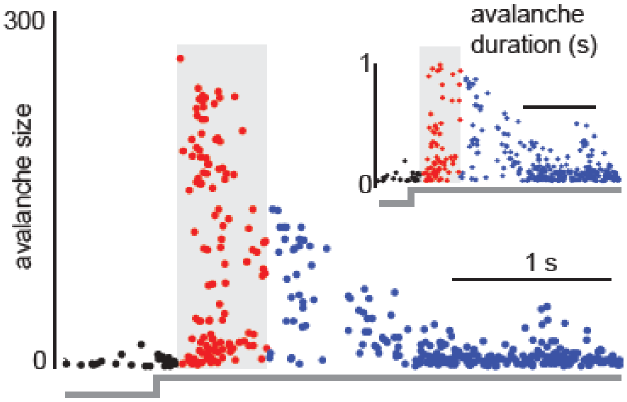

Figure 9 – Graphs showing avalanche size and duration during evoked activity. Ongoing activity is represented in black, transient response in red and steady-state response in blue. The grey bars beneath the graphs represent the signal sent by the stimulus computer to indicate stimulus onset. Note the characteristic bimodal distribution of avalanche size and duration during the transient response (red) compared to the steady-state response (blue).

From this graph alone it can be seen that there are marked differences between the ongoing, transient and steady-state response. There is little activity pre-stimulus in the ongoing stage, a large spike in neural activity which is then followed by a downward slope in activity due to activity until the steady state response. Note that in both duration and size the transient has a bimodal distribution of avalanches, a characteristic of supercritical neuronal networks.

To examine criticality within this graph, three graphs are made from the same avalanche data shown above with the same color code using the method described in the Data Analysis section. As discussed earlier a property of criticality in neural systems is power-law distribution of observables. Note that the scale for Figure 8 is logarithmic and therefore the plots across each graph are power-law distributed. The grey data points on the graphs represent a time-jittered control to ensure that our neuronal avalanche data was indeed temporally related in a meaningful way. We found that it appears that ongoing activity is critical in accordance with previous theory and experimentation. For the first time experimentally however, we show that the steady-state response to visual stimuli appears to be critical as well – an indication that the dynamic range may be maximized as well as broadened.

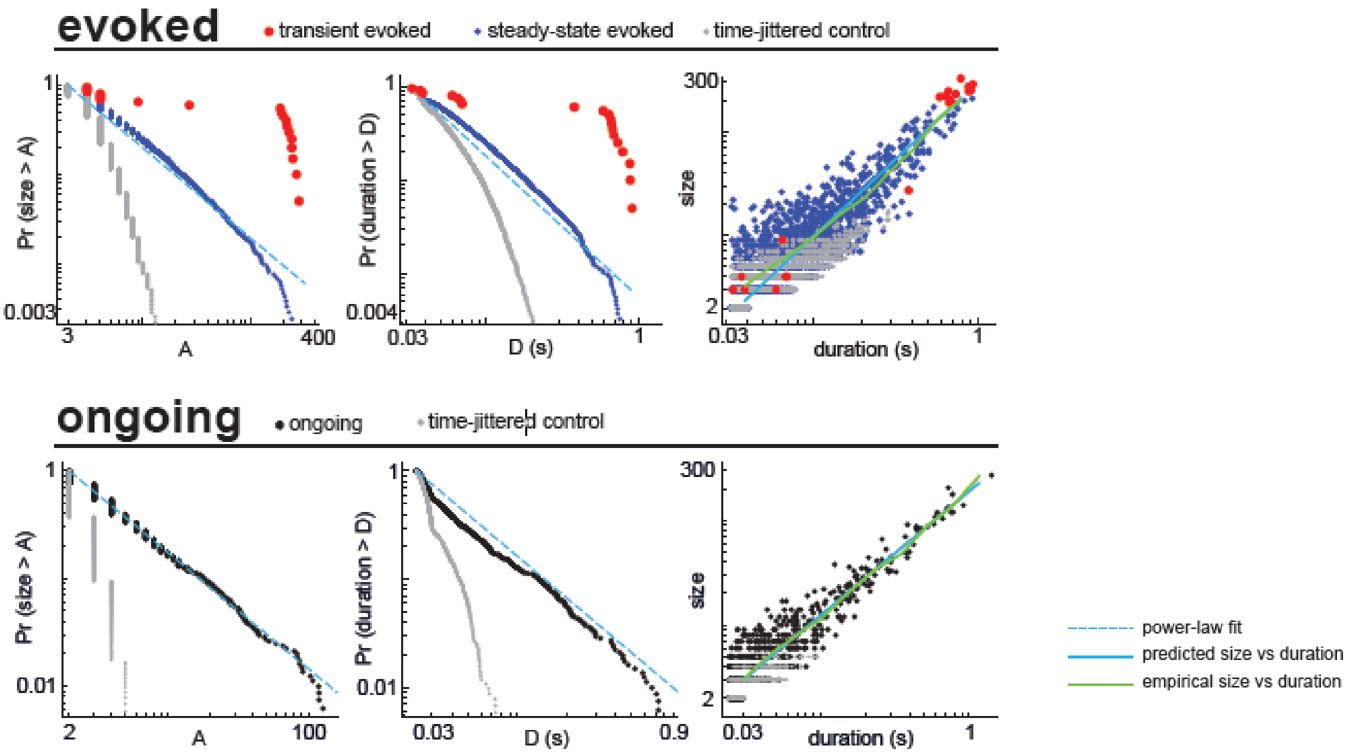

Figure 10 – Top: Two graphs showing the power-law distribution of avalanche size and duration for evoked data (blue) next to a graph of best-fit to the power law function as discussed in the Data Analysis section. A connection should be made between the noted bimodal distributions of size and duration in Figure 7 to the transient data (red) presented in these graphs as the bimodal distribution of both size and duration can be more clearly seen.
Bottom: Two graphs showing the power-law distribution of avalanche size and duration for evoked data next to a graph of best-fit to the power law function as discussed in the Data Analysis section. This data confirms previous studies which found critical behavior in ongoing, spontaneous activity.
For both the top and bottom plots, the gray points are based on a control analysis in which the times of LFP peak events are randomized, thus destroying temporal correlations across electrodes. The dramatic difference between the gray distributions and the blue and black distributions indicates that temporal correlations play an important role in determining the shape of these distributions.

When looking at the three different data types: ongoing, transient evoked and steady-state evoked three observations can be made. (1) That in accordance to previous research, ongoing activity in the brain is critical, (2) steady-state evoked activity is critical and (3) that transient evoked activity is not-critical, but supercritical which is consistent with theorized models. Evidence for this can be further seen in the graph below which summarizes deviation from best fit from best fit power-laws for both size and duration in avalanches for ongoing, steady-state and transient evoked activity. We found that this is evident in all three types of stimulus set: naturalistic movies, scanning dots and LED flashes. This suggests that this effect is fairly general to all types of visual stimulus.

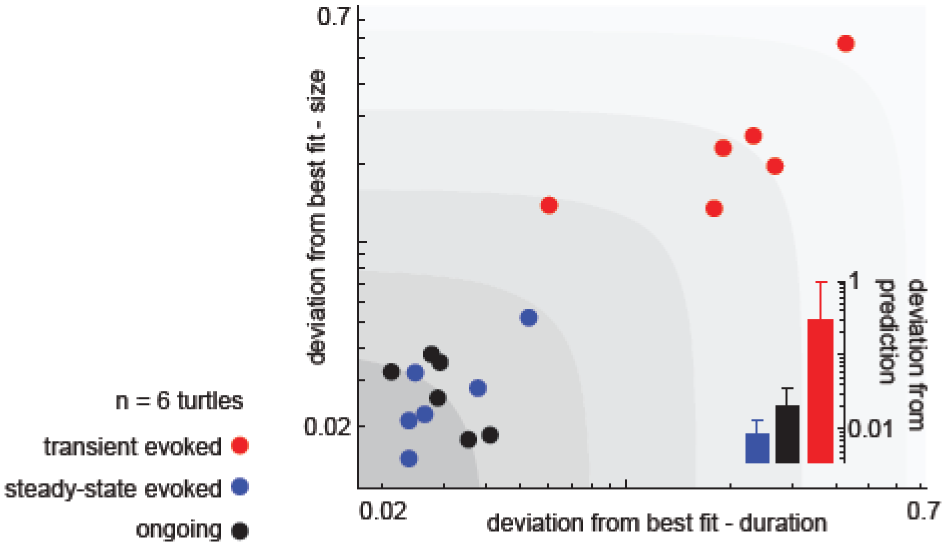

Figure 11 – Graph of deviation from best fit using the κ value from both size and duration. This graph shows that both the ongoing and the steady-state response were operating near criticality while the transient response was super critical.

Conclusions

In previous studies of neuronal networks it has been shown that criticality was present during spontaneous, ongoing activity. However, there has yet to be experimental data that indicates that the network exhibits criticality during stimulus driven activity. It was also shown that adaptation served to maintain neuronal activity in a critical-like state and that there were functional benefits of both adaptation and criticality on the dynamic range of the network. In this experiment we have proven experimentally for the first time that sensory driven cortex dynamics maintain signatures of criticality, except for a small period called the transient response that occurs after stimulus onset. Our data suggests that this transient period, thought to be a period of adaptation, is not critical, but rather supercritical. This data provides a strong case that adaptation maintains cortical visual processing at criticality.

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