

Research Article

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Reduction in Noise Correlation is Associated with Improved Behavioural Performance

Abstract

Background: Visual perception constitutes the dominant method by which we process our environment, yet the neuronal substrates that underlie visual perception in the brain are not well understood. Noise correlation, defined as the correlation in non-stimulus evoked activity between neurons, has been shown to impact both encoding and decoding processes of visual stimuli. We wanted to determine whether changes in noise correlation can predict behavioural performance in a coherent motion-detection task.

Methods: Two macaque monkeys (*Macaca mulatta*) were trained in a coherent motion-detection task, where they learned to fixate on a screen and anticipate the onset of a motion coherence stimulus. During this task, spike activity from pairs of neurons of the middle temporal area (area MT) were recorded and data was analyzed using MATLAB. Specifically, we examined noise correlation as a function of time and success rate in the task.

Results: We found a decrease in the correlation in activity between neurons in area MT prior to the onset of the motion coherence stimulus. This decrease was accompanied by improved behavioural performance in the motion coherence-detection task.

Limitations: The activity in pairs of neurons may not accurately represent overall activity in a population of neurons. In addition, control experiments to better assess the nature of the common input that leads to a reduction in noise correlation were not conducted.

Conclusions: Despite these limitations, we have shown that a reduction in noise correlation prior to stimulus onset is accompanied by improved behavioural performance, suggesting that noise correlation may be a critical parameter that can aid in our understanding of how visual perception occurs in the brain.

Introduction

"Sensation is an abstraction, not a replication, of the real world", stated the neuroscientist, Vernon Mountcastle. (1) This statement is particularly relevant to visual perception, the dominant method by which we process our surrounding environment. Yet it is not well understood how this abstraction of stimuli into visual perception occurs in the brain.

Multiple levels of analysis can be employed to understand this question. One can either look at how information is encoded in individual neuronal activity, or in the correlated activity between neurons. (2) There are several reasons why examining correlated activity between neurons is of interest. Noise correlation, defined as the correlation in activity between neurons that is non-stimulus evoked, is thought to limit the amount of information that can be encoded by a neuronal population. (3) This limitation can occur even with weak Pearson's correlation coefficients of $r = 0.1$, as noise correlations can impede stimulus-relevant signal decoding in systems that average neuronal activity. (4) Averaging neuronal activity facilitates signal detection by minimizing noise best when the noise between neurons is independent (noise correlation is equal to 0). In cases where the noise is correlated, averaging fails to remove it.

However, averaging is not the only possible mechanism by which signals can be decoded. For certain noise models, correlations may in fact improve coding accuracy. (5) It has also been found that only correlations proportional to the derivatives of the tuning curves of the neurons in question are information-limiting, so the overall pairwise correlation may not be a meaningful indication of information-coding capacity. (6)

Finally, reductions in noise correlation have been proposed to be the main

mechanism by which attention improves performance on tasks that involve responses to visual stimuli. (7, 8) Combined, this information suggests that noise correlation is a functionally relevant parameter that may impact both encoding and decoding processes in the brain.

The goal of the present study was to determine whether changes in noise correlation over time would be observed in the middle temporal area (area MT) of macaque monkeys performing a coherent motion-detection task, where motion coherence is defined as the degree to which all particles within a patch are moving in the same direction, and whether this change would be associated with changes in behavioural performance.

Methods

Experimental Setup

Activity from pairs of neurons in area MT were recorded from two macaque monkeys performing a coherent motion-detection task that they were previously trained in. Monkeys visually fixated within a 2° square fixation window and the time of fixation was designated $t=0$ or t_0 . Following fixation, particles within either one or both of two patches presented onscreen that were initially moving in random direction began moving in a coherent manner (of varying degree) towards a specific direction (Fig.1). The onset of this coherence varied per trial between 200 ms to 1000 ms from the time of fixation, and the motion coherence pulse lasted for 50 ms. Once the monkey detected the onset of coherence, it had to release a lever within 200 ms to 800 ms from the pulse onset to receive a reward. Trials where the lever was released within this time window from the onset of coherence were deemed successful.

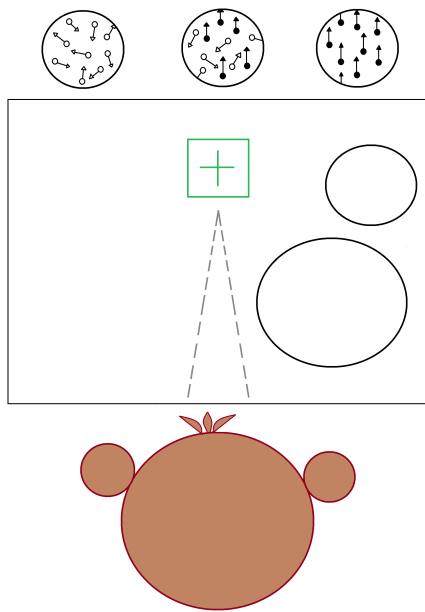


Fig. 1. Top panel presents motion coherence stimulus, with increasing degree of coherence in particle movement from left to right (0%, 50%, 100%). Bottom panel presents experimental set-up. Monkey fixates (represented by dotted lines) within square window marked by cross. After a certain period of time, particles in either or both patches presented onscreen begin moving in a coherent manner.

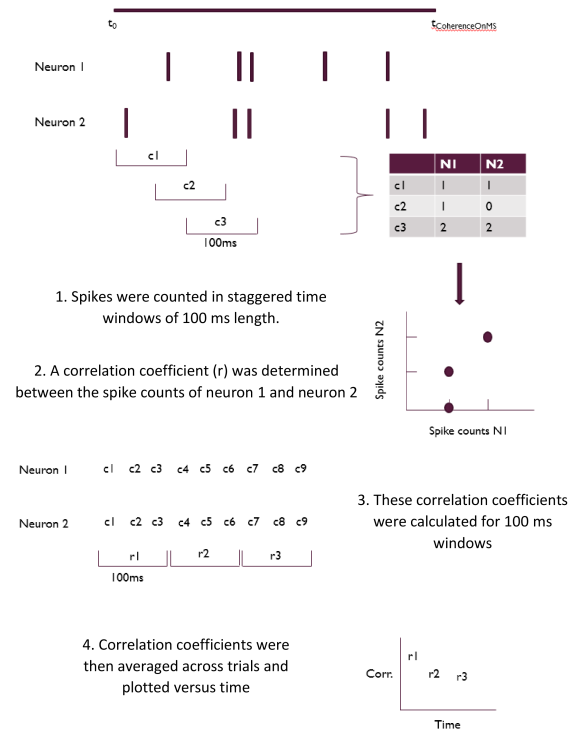


Fig. 2. Schematic of MATLAB analysis. For each trial, the number of spikes in staggered 100 ms windows was counted, generating the values c_1, c_2, \dots for each neuron. Correlations were calculated between the values c_1, c_2, \dots in 100 ms intervals (correlation windows). These correlations were averaged across trials and plotted versus time.

Extracted Data from Experimental Structures

Extracted data from each experiment used in our MATLAB analysis included the spike times of two recorded neurons, neuron 1 and neuron 2, the time of coherence onset, and whether the lever was released. These data were extracted per trial, from all conditions (coherence in either one or both patches), from each experiment. Since our aim was to detect changes in noise correlation between pairs of neurons before the onset of a motion stimulus in monkeys trained to expect a stimulus, we did not differentiate between the different conditions, as the exact nature of the eventual stimulus was not expected to change the prior activity of the neurons. We analyzed 49 experiments for a total of 22,486 trials.

Noise Correlation as a Function of Time

To evaluate how noise correlation changes as a function of time within a single trial, we first generated a list of spike counts, one for each neuron. The number of spikes was counted in staggered 100 ms windows, in a “moving boxcar” manner, from the fixation time t_0 (included), to the time of motion coherence onset, coherenceOnMS (excluded). Once these lists were generated, we calculated the Pearson’s correlation coefficient for the spike counts between neurons within 100 ms windows, termed correlation windows (Fig. 2), restricted to the same time frame as the list of spike counts (t_0 to coherenceOnMS). These calculations were made for each trial. Correlation windows in which a correlation coefficient could not be calculated because there were no changes in spike count in either neuron were excluded from further analysis. These correlation coefficients were then averaged across all trials in all conditions and all experiments. The average correlation coefficient for each correlation window was then plotted as a function of time. Standard error means (SEM) were determined for each correlation window.

Task Performance

To assess whether changes in noise correlation are associated with behavioural performance, we measured behavioural performance as the fraction of successful trials over total trials, and plotted these measures as

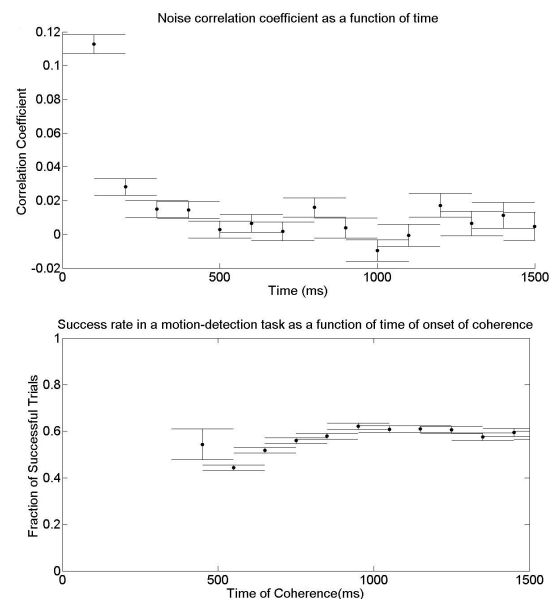


Fig. 3. Top: averaged correlation coefficients in 100 ms bins as a function of time. Bottom: fraction of successful trials, in which a lever was released following detection of motion coherence, as a function of the time of motion coherence onset. Plotted S.E.M. bars per bin.

a function of the time of motion coherence onset. These values were then binned in 100 ms windows. Standard error means were determined for each bin as was done for the correlation coefficients, assuming that each

trial follows a Bernoulli distribution where a successful trial has a value of 1 and a failed trial has a value of 0.

Correct Versus Failed Trial Separation

To determine if changes in noise correlation would differ between correct trials and failed trials, we performed the same analysis as described in 'Noise correlation as a function of time', but separately for correct versus failed trials.

Results

To determine if changes in noise correlation in area MT of macaque monkeys were observed during a motion-detection task, we compared spikes recorded from pairs of neurons from the time at which the monkey visually fixated on a point (inclusive) to the time of onset of the motion stimulus (exclusive). Correlations were calculated per correlation window of 100 ms. We found a decrease in noise correlation, from a value of 0.11 to 0, within 500 ms from the time of fixation. After this period, the activity between neurons remained independent ($r=0$) (Fig. 3, top).

To see if this reduction in noise correlation was associated with changes in behavioural performance in the motion-detection task, we compared the success rate, a ratio of successful trials over total trials, to the onset of motion coherence which varied in each trial. We observed a modest increase in the fraction of trials that were successful, from 0.44 for trials with coherence times between 500 ms and 600 ms to 0.60 for trials with coherence times at approximately 1 second (Fig. 3, bottom). The success rate for trials with coherence times between 400 ms and 500 ms was calculated to be 0.54, and thus does not follow the same trend; however, since there were very few trials with coherence times between 400 ms and 500 ms, the discrepancy could be attributed to error due to small sample size. Comparing the two graphs in Fig. 3, we see that noise correlation decreased rapidly within 500 ms from fixation time, where very little data for success rate is available. Between 500 ms and 1000 ms, where success rate increased, there is a moderate negative correlation between average noise correlation and success rate ($r=-0.42$). Both values then plateaued, where noise correlation equaled to 0 and success rate equaled to 0.6. These results suggest that a reduction in noise correlation in area MT may be

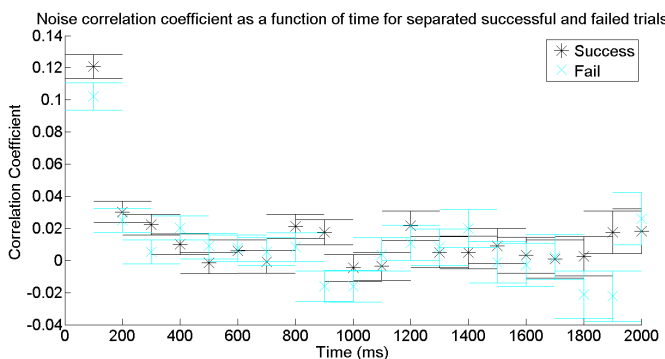


Fig. 4. Averaged correlation coefficients in 100 ms bins as a function of time, separated for successful (black) versus failed (grey) trials. There is no significant difference in the changes in correlation with time between successful and failed trials, although the initial average correlation coefficient for successful trials (0.12) is slightly higher than that of failed trials (0.10). Plotted S.E.M. bars.

associated with improved behavioural performance in the coherent motion-detection task.

To determine if changes in noise correlation differed between successful trials and failed trials, we assessed noise correlation separately for correct versus failed trials from the time of fixation to the onset of motion coherence. There appeared to be no significant difference in the time course of noise correlation between correct and failed trials. There is, however, a

small difference in the initial noise correlation value between correct and failed trials, which were 0.12 and 0.10, respectively (Fig. 4).

Discussion

It is important to note that while previous experiments (4, 7, 8) calculated noise correlations across trials for a pair of neurons, thus measuring correlations in trial-to-trial fluctuations, we chose to calculate the noise correlation between a pair of neurons for each trial before averaging the correlations across all trials. We chose this because our interests lay primarily in the change in noise correlation as a function of time during anticipation of a stimulus, rather than in trial-to-trial variability. Nevertheless, we obtained initial noise correlations close to those previously reported (7), although a direct comparison of our results would not be appropriate due to the differing methods of calculation.

Our observed reduction in noise correlation appeared to be associated with increased success rates, but the progression did not vary between correct versus failed trials. These results suggest that while noise correlation may facilitate encoding of a visual stimulus, thereby increasing the probability of a successful trial, it may not be the distinguishing factor between correct versus failed trials. In other words, additional parameters, which have been found to be related to behavioural output, such as firing rates, may play a greater role in determining a successful trial. (9) These results contrast a previous study that has shown that behavioural performance in orientation-change detection tasks is improved primarily by reducing noise correlations in visual area V4. (7) It is possible that higher-order processing structures, such as area MT compared to V4, may incorporate a greater number of parameters in processing a visual stimulus. This would reduce the contribution of an individual parameter, such as noise correlation.

The increased success rate was seen in trials with coherence onset between 500 ms and 1 second after fixation, and success rate appeared to plateau at roughly 800 ms, while the average interneuronal correlation coefficient decreased to 0 by 500 ms. A delay of 300 ms from the time at which the noise correlation plateaued to the time at which the success rate plateaued indicates that these two phenomena cannot be said to occur on the same time scale. This delay may have arisen from integration of the noise correlation by downstream structures to area MT. In other words, a delay of at least 300 ms from the time of fixation to the onset of motion coherence may be sufficient to integrate the reduction in noise correlation in area MT in order to improve behavioural performance. Unfortunately, there were very few trials with coherence times before 500 ms and no trials with coherence times before 400 ms. Therefore, we have insufficient data to make conclusive statements.

While the lack of distinction between successful and failed trials when the correlation coefficients were averaged and plotted separately for each trial does not suggest that decreased correlation coefficients lead to improved performance at responding to stimuli, it does not preclude the possibility of a relationship. A potential experiment to test the relevance of noise correlations could involve maintaining weak activity correlations in area MT as the animal performs the same task. If a decrease in correlation coefficient is truly necessary to see an increase in performance, we would expect the increased performance to be abolished. However, we do not have a suitable method for manipulating correlated activity in the brain, as we do not yet know the mechanisms by which interneuronal correlation is modulated. Nevertheless, manipulation of noise correlation has been attempted with optogenetic methods. (10)

The nature of the common input that modulates noise correlation in area MT was not investigated in this study. It is possible that this common input reflects a change in attentional state following fixation. (7) However, given that our data analysis was restricted to the time from fixation to the onset of motion coherence, we did not have an inattention control. With respect to this limitation, it would be of interest to examine noise correlation prior to fixation as a potential measure for inattentiveness.

The observed reduction in noise correlation may also relate to an expected

change. In other words, visually fixating at a point that does not predict a presentation of a stimulus does not lead to a reduction in noise correlation, but fixating at a point that does predict a presentation of a stimulus does lead to a noise correlation reduction at fixation time.

Conclusion

Understanding the molecular basis of this common input is imperative to establishing a causal relationship between noise correlation and behaviour. One postulation would be that upstream structures release neuromodulators such as acetylcholine, which have been functionally associated with attention (11), thus regulating the activity of neurons from area MT. In addition to previously mentioned optogenetic approaches, it would be feasible to use pharmacological molecular targets in order to assess causality.

It is important to keep in mind while discussing these results that activity from pairs of neurons may not accurately represent activity from a population of neurons. (3) Technique wise, it is difficult to record from multiple neurons simultaneously while still being able to distinguish individual neuronal activity. Extracellular recordings or electroencephalograms only provide summed activity from a focal point. In addition, the data we have presented is only correlational, not causal.

Further investigation is required to better understand how noise correlation can influence behaviours and what mechanisms modulate noise correlation. In the present study, we see a reduction in average noise correlation between pairs of neurons before the onset of an expected stimulus that is associated with improved behavioural performance.

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