RESEARCH ARTICLE

Neuronal spiking is better than bursting at predicting motion detection in area MT

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Keywords:
Spiking: *Spiking is the brain's mechanism to transmit stimulus information by a rate code (spikes per unit time).*
Bursting: *Bursting is a dynamic state in which a neuron repeatedly fires a number of action potentials within a time period (1).*
Middle Temporal Visual Area (MT): *The MT area of the macaque monkey is part of the extrastriate visual system, and is concerned with processing visual motion.*
aROC: *The area under the receiving operator characteristic curve is a graphical technique that determines the level of correlation between two events.*
Coherent Motion: *When a percentage of the random dot patch (RDP) moves in the same direction, the result is coherent motion. This is depicted in Fig. 1.*

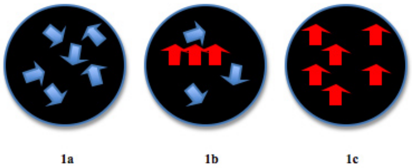

Fig. 1
This is a depiction of varying coherent motion presented to a neuron's receptive field. 1a depicts 0% coherent motion. 1b depicts 50% coherent motion. 1c depicts 100% coherent motion.

Abstract

Background: The middle temporal visual area (MT) is widely studied in visual processing and in integration of motion signals to form general perceptions. The objective of this study is to determine whether neuronal bursting in area MT of monkeys is more predictive of motion detection than neuronal spiking.

Methods: Two *Macaca mulatta* (macaque) monkeys were trained in Dr. Erik Cook's lab to detect coherent motion while connected to microelectrodes that determined their neuronal spiking activities. Using MatLab, we manipulated the collected data to determine whether spiking or bursting is more predictive of motion detection.

Results: We repeatedly found that neuronal spiking in area MT is better than bursting at predicting motion detection in macaques ($p < 0.01$).

Conclusions: Therefore, our results suggest that area MT neurons do not fire behaviourally-meaningful bursts in response to coherent motion. This finding is useful for learning about the visual processing pathway, and how information is coded in the brain.

Limitations: A key limitation of this study is that we did not exclude any experiments from analysis to control for quality of the collected data, perhaps leading to confounding factors.

Introduction

There are many ways to look at the temporal features of a neuron's spike train and determine its significance to an animal's behaviour (2). For example, studies have looked at the average spiking rate after presentation of stimulus without particular attention to the frequency of spikes or the number of inputs that a neuron integrates. Some have focused more on the firing pattern of groups of neurons rather than isolated neurons while others have looked at neural bursting activity. This paper will further look at bursting, along with average spiking.

Research in the pyramidal neurons of the hippocampus best highlights the bursting phenomenon (3). In this area, bursts of 2 – 6 spikes for a duration of 25 milliseconds or less have been tracked through extracellular recordings (4). The spiking rate of a presynaptic neuron at the central synapse is not predictive of the spiking rate at the postsynaptic neuron; this supports the notion that bursting may be a better predictor of behaviour than the average spiking rates (5). This was first studied in motoneurons and Mauthner cells, and later in different brain areas like the primary visual cortex (V1) (2). For example, both average spiking rate and bursting increase when a stimulus is presented to a V1 neuron's receptive field. However, synapses are sometimes "unreliable", which means that an action potential at the presynaptic neuron does not trigger an action potential at the postsynapstic neuron. Though this poses a problem with isolated spikes, rapid successions of presynpatic input onto the postsynaptic neuron can increase the probability of an action potential firing at the postsynaptic neuron. Hence, bursting in a V1 neuron can encode more relevant information than isolated spikes in a V1 neuron, which is more indicative of noise (2).

The middle temporal visual area (MT), an area of extrastriate visual cortex, plays an important role in visual processing. A major input to this region is a magnocellular-dominated projection from layer 4B of V1. The MT visual area also receives projections from V2 and V3 - which are downstream of V1 - and directly from the lateral geniculate nucleus. Each MT neuron is tuned to a particular receptive field, and selective for a motion direction and speed to which it responds most vigorously. Area MT projects to downstream regions such as the ventral intraparietal area (VIP) and the medial superior temporal (MST) area (6). The MT region is crucial in motion perception, control of eye movements, and in integration of motion signals into a general perception (6). Since bursting has been shown to play an important role in V1, this paper looks at whether bursting also plays a role in area MT.

In this paper, we will explore two research ideas with respect to neuronal activity in area MT. Firstly, we will determine which bursting parameter for neurons in area MT is most predictive of detecting coherent motion. Secondly, we will compare the average spiking rate and bursting of neurons in area MT and determine which of the two is more predictive of motion detection in *Macaca mulatta* (macaque) monkeys.

Methods

Behavioural Task

Dr. Cook's lab trained two macaques to detect coherent motion while connected to tungsten microelectrodes, which recorded their neuronal spiking activities. Each experiment used one monkey, and each experiment consisted of a varying number of trials. Each trial recorded the activity of two different neurons, neuron 1 and neuron 2, from the same hemisphere of the monkey in question. Data was obtained from 19540 trials over the course of 50 experiments. The lab determined the location of each neuron's receptive field, along with its preferred speed, orientation, and direction of stimulus before the beginning of an experiment. Then, Random Dot Patches (RDP) were presented to that neuron's receptive field with increasing coherence, starting at 0% and adhering to the neuron's preferences.

There were three conditions in each trial. Condition 1 represented coherent motion in the receptive fields of both neuron 1 and neuron 2. Condition 2 presented coherent motion only in the receptive field of neuron 1. Condition 3 presented coherent motion only in the receptive field of neuron 2. Anywhere between 500 and 10,000 ms after the onset of RDP presentation, the RDP was presented with coherent motion in the receptive field(s) for 50 ms (Fig. 2). The monkeys were trained to maintain a fixation point on the screen, and release a lever for a juice reward if they correctly detected coherent motion. A trial was considered correct only if the monkey released the lever within a window of 200-800 ms after coherent motion turned off, and incorrect in every other instance. All trials were organized into two groups for analysis: correct and incorrect. We analyzed the electrophysiological data based on the 100 ms time window after coherent motion was turned off.

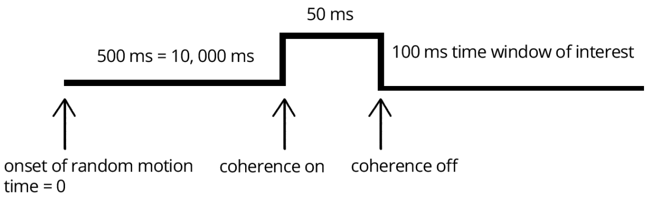

Fig. 2
This is a graph of the presented stimulus on a timeaxis. There are four times that are important for this experiment:
1) onset of random motion - this is when the RDP is presented to a neuron's receptive field at time 0
2) coherence on – this denotes when coherent motion is presented in a receptive field
3) coherence off – this denotes when the coherent motion stops
4) the 100 ms after coherence off – this was used for analysis.

Analysis of Data

We used a time period of 100 ms for our analysis because previous studies have reported that neural–behavioural covariation is greatest for this time window (7) . We used values for the standard area under the receiving operator characteristic curve (aROC) to determine the probability of motion detection that is correlated to a specific bursting parameter or to a spiking activity. If an aROC value of 0.5 is returned, this suggests that there is no correlation between the number of correct trials and the neuronal activity in question. However, aROC values greater or less than 0.5 suggest a greater predictive capacity (8) and correlation between the number of correct trials and neuronal activity. What matters is not whether the aROC value is greater or less than 0.5, but the absolute difference between the aROC value and 0.5 (ie. aROC values of 0.6 and 0.4 have an equal predictive capacity). The higher the absolute difference between 0.5 and the aROC value, the higher the predictive capacity (8). The bursting parameters we used varied from 1 – 5 spikes for 10 – 100 ms with 10 ms steps.

In order to produce aROC values for the different bursting parameters, we first calculated the distribution of the number of bursts within the 100 ms time period after coherence was turned off for both correct trials and incorrect trials averaged over both neurons in condition 1. We inputted these distributions into the MATLAB function detect probability, which outputted an aROC value. This function was written by members of Dr. Cook's lab. These values could be compared across different bursting parameters, allowing us to determine which resulted in the best covariation with behaviour. The same metric was used to analyzed the covariation between average spiking rate and the behavioural outcome. This allowed us to determine whether bursting rate or spiking rate is more closely correlated to correct motion detection in monkeys.

Results

1) Different Bursting Parameters in Condition 1, Neuron 1 and Neuron 2 combined

We determined one aROC value for each of the different combinations of bursting parameters, which produced a 10 by 5 matrix (Fig. 3). Fig. 4 graphically depicts the aROC value for a given burst parameter. As evident by Fig. 3 and Fig. 4, the highest aROC value we obtained is 0.5742, for the bursting parameter 1 spike/10 ms. The second highest aROC value is for 1 spike/20 ms, and the third highest aROC value is for 2 spikes/20 ms. (Fig. 3 and 4). For further analysis, we discounted the aROC values for bursts with only 1 spike, because we believe a neuronal burst should have multiple spikes. Instead, we used the aROC value obtained for 2 spikes/20 ms.

With the bursting parameter 2 spikes/20 ms, we calculated the average number of bursts in a trial (Fig. 5). We found the average number of bursts for correct trials to be 1.6371, and the average number of bursts for incorrect trials to be 1.2537. After applying the t-test for the significance of the difference between the means of two independent samples, the p-value we obtained for this result is less than 0.01. All p-values in this paper were obtained through the same statistical test.

	1 spike	2 spikes	3 spikes	4 spikes	5 spikes
10 ms	0.5742	0.5593	0.5348	0.507	0.502
20 ms	0.5694	0.5666	0.556	0.5393	0.51
30 ms	0.5642	0.5636	0.5599	0.5549	0.5263
40 ms	0.562	0.5633	0.5595	0.5516	0.5431
50 ms	0.558	0.5603	0.5597	0.5559	0.5482
60 ms	0.5555	0.555	0.5584	0.559	0.5465
70 ms	0.5578	0.5577	0.5609	0.5539	0.5461
80 ms	0.5545	0.5544	0.5538	0.5537	0.5472
90 ms	0.5528	0.5528	0.5525	0.5522	0.5428
100 ms	0.5526	0.5526	0.5526	0.5534	0.5436

Fig. 3

This is the matrix obtained when we used different bursting parameters. The ones highlighted in red gave the highest aROC values.

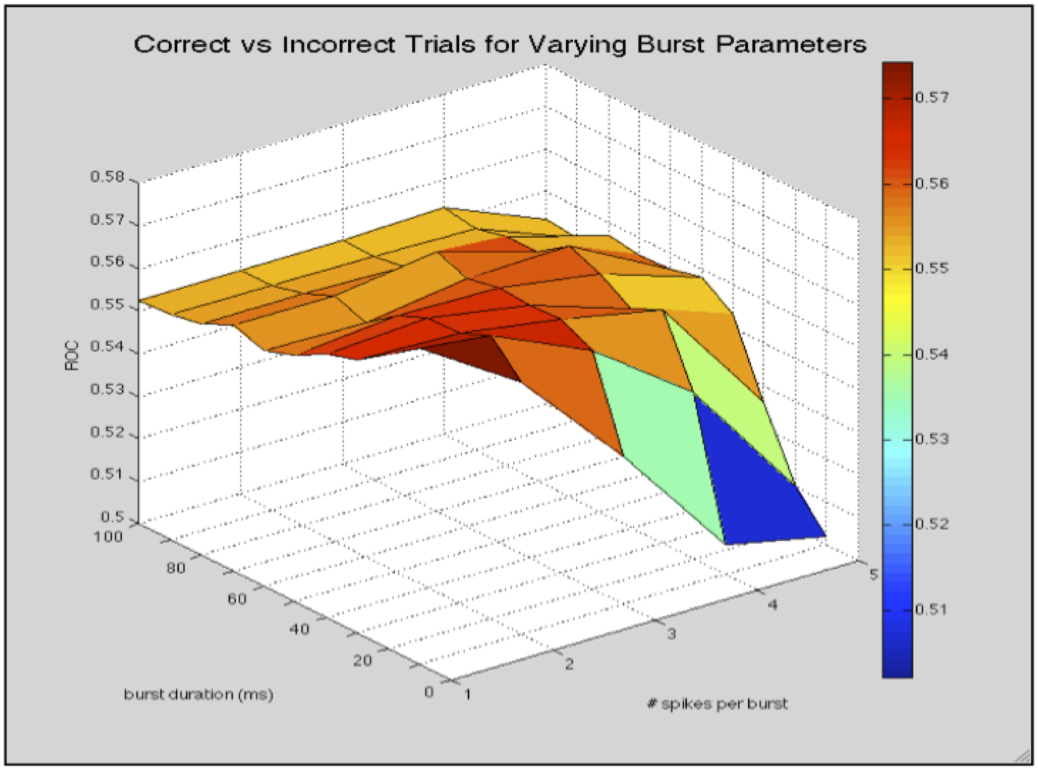

Fig. 4

This graph represents the same information as the matrix in Fig. 1.

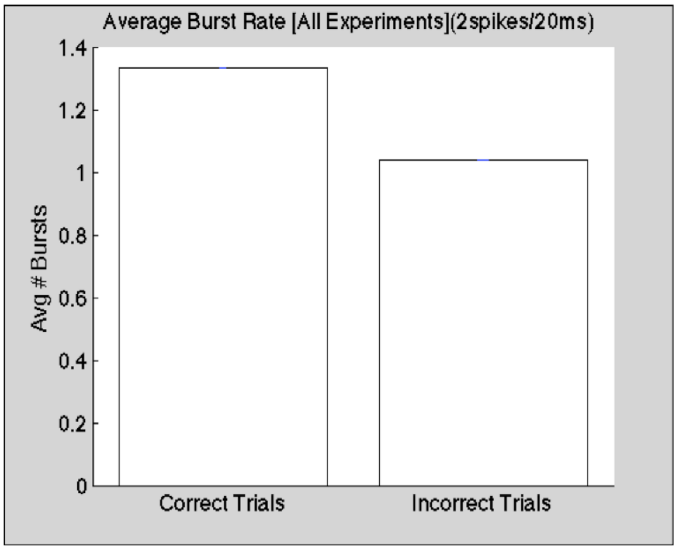

Fig. 5
This bar graph depicts the average number of bursts per correct trial and incorrect trial. As our obtained p-value was much smaller than 0.01, the plotted error bars are difficult to see.

As a post-hoc analysis, we wanted to see if the percentage of coherence in the RDP would alter our results. Of all 50 experiments, we found five experiments that represent the highest level of coherence: 80% coherent motion in both receptive field 1 and receptive field 2. When we ran our analysis again only for these five experiments, we found that the aROC values were higher in general. However, the best bursting parameters remained the same: 1 spike/10ms had an aROC value of 0.6715, 1 spike/20 ms had an aROC value of 0.6503, and 2 spikes/20 ms had an aROC value of 0.6454.

We calculated the average number of bursts only for the five experiments that had 80% coherence in the two receptive fields for the bursting parameter 2 spikes/20 ms (Fig. 6). We found the average number of bursts for correct trials to be 1.3317, and the average number of bursts for incorrect trials to be 1.0390 ($p < 0.01$).

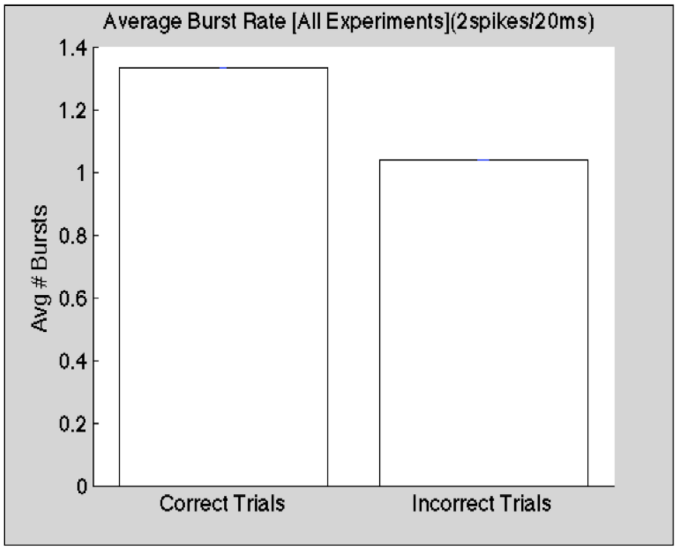

Fig. 6
This bar graph depicts the average number of bursts per correct trial and incorrect trial for the 5 experiments with 80% coherence in receptive field 1 and 2, $p < 0.01$.

2) aROC value for Isolated Spiking Activity

When the “detect probability” function was run for isolated spikes and averaged over neuron 1 and neuron 2 of all experiments, we obtained an average aROC value of 0.5961. We conducted the same post-hoc analysis (as described in section 1 of results) for the five experiments with 80% coherence in both receptive fields, and found an aROC value of 0.7163.

Discussions

After creating a matrix with different bursting parameters, we found the highest aROC values for 1 spike/10 ms, 1 spike/20 ms, and 2 spikes/20 ms. This suggests that these bursting parameters have the highest predictability of behaviour. The aROC values we obtained for 2 spikes/20 ms and for average spiking under Condition 1 are 0.5666 and 0.5691, respectively. Since both can be rounded to 0.57, the difference between spiking and bursting in Condition 1 is not significant. For the bursting parameter 2 spikes/20 ms, we found the average number of bursts for correct trials to be 1.6371, and the average number of bursts for incorrect trials to be 1.2537 ($p < 0.01$), asserting that there is a significant difference in neuronal bursting between correct trials and incorrect trials.

In order to determine if the percentage of motion coherence in the RDP played a role in our results, we analyzed the experiments that presented 80% coherence (the maximum coherence across all experiments) in both receptive fields. We found five experiments that satisfied this condition; when we ran our analysis for the different combinations of bursting, we found the same bursting parameters (1 spike/10 ms, 1 spikes/20 ms and 2 spikes/20 ms) produced the highest aROC values. However, these aROC values were still not as high as the one obtained for spiking in these five experiments, suggesting that bursting is not better than spiking at predicting monkey behaviour - even when motion coherence is controlled for.

No experiments were excluded from analysis, perhaps contributing to potential confounding factors. There are several reasons why an experiment should be excluded: if the monkey pulled the lever before coherence was turned on or if the number of trials in an experiment was too low, for example. Furthermore, the aROC values obtained were not used to calculate a sensitivity index, which would determine the signalling reliability of the neuron (7). This type of analysis would compare the number of bursts and spikes before coherence was turned on and after coherence was turned off. It would also be worthwhile to determine if these neurons experience periods of quiescence, a characteristic of bursting neurons, and if these neurons were bursting in groups rather than in isolation.

Conclusions

Our results suggest that neuronal bursting is not behaviourally-relevant in area MT of macaques. The correlation between burst rate and behavioural outcome is weaker than the correlation between spike rate and outcome, indicating that single spikes carry more valuable information about motion to downstream processing areas. This result is congruent with Lisman *et al.*'s report on bursting in area MT, which concluded that, “if only bursts are considered, there is a marginally poorer estimate [of direction]. In this case it is clear that single spikes carry information” (2). Our finding enhances our understanding of how behaviorally-relevant information about motion is encoded by area MT neurons, and could have implications for how motion is processed in downstream areas with more complex response properties.

Acknowledgements

We would like to thank Dr. Cook and his lab at the Department of Physiology for teaching us how to use MATLAB and for guiding us through all the steps of this project.

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