The mammalian cortex's dendritic spikes in vitro and in vivo

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Bhanushali S. The mammalian cortex's dendritic spikes in vitro and in vivo. J Clin Psychiatry Neurosci.2022; 5(4):41-2.

ABSTRACT

Dendritic spikes have been observed in various neurons in various brain regions, from the neocortex and cerebellum to the basal ganglia, in the half-century since their discovery by authors and colleagues. Dendrites have a fantastically diverse but stereotypical repertoire of spikes, which are sometimes specific to dendrite sub regions. Despite their prevalence, we know very little about their role in animal behavior. The purpose of this article is to survey the entire spectrum of dendritic spikes found in excitatory and inhibitory neurons, compare them in vivo versus in vitro, and discuss new studi-

INTRODUCTION

he action potential was named after du Bois-discovery reymond's of "negative variation" in the mid-nineteenth century. Since then, understanding of the axonal Action Potential (AP) has been refined over many years, culminating in the hands of Hodgkin and Huxley in the form of a biophysical model. Dendrites, neuroscientists hypothesised, would also fire action potentials (here after, spikes). They proposed that dendritic spikes play an important role in synaptic integration by amplifying weak distal inputs. Surprisingly, visionary ideas emphasizing the importance of dendritic spikes in neural computation began to emerge concurrently with the revolutionary invention of the perceptron. By stimulating climbing fibers in the anaesthetized cat cerebellum, authors and colleagues elicited spikes at the distal regions of Purkinje cell dendrites. With the single extracellular electrode used in these experiments, it was difficult to determine the source of the spikes conclusively. One possibility is that the action potential started at the axon and spread to the dendrites. Author preferred the alternative explanation, in which the spikes were initiated at the dendrite and propagated towards the soma, based on the waveform of the recorded spikes. The author provided evidence for dendritic initiation of spikes by measuring their latency in the alligator cerebellar cortex at various depths. Author and colleague's work eventually led them to record these spikes intracellularly, directly from the dendrites. They later discovered that these spikes were caused by calcium channels.

-es describing dendritic spikes in the human cortex. We concentrate on neocortical and hippocampal neurons and present a strategy for identifying and comprehending the broader role of dendritic spikes in single-cell computation.

Key Words: Dendrites

Even today, performing these pioneering in vivo intracellular dendritic recordings are difficult, which explains why only a few in vivo studies use electrodes to record directly from the dendrites. Furthermore, in living animals, dual recordings with one electrode at the cell body and another at the dendrite are nearly impossible. Because of this limitation, the experimental basis for understanding signaling between the dendrite and the axosomatic region has been primarily provided by in vitro studies with dual recordings. A detailed description of the function of dendritic spikes during relevant behavioural events. Dendritic spikes are biophysically caused by a supra linear increase in membrane potential caused by regenerative inward currents. The duration of the various classes of dendritic spikes varies greatly, ranging from a millisecond to hundreds of milliseconds. Some of them, known as intrinsic spikes, are activated when the dendritic membrane crosses a voltage threshold set by voltage-gated ion channels. Na+ spikes/spikelets, Ca2+ spikes, Low-Threshold Spikes (LTS), and Ca2+ plateau-potentials are examples of these (note that back-propagating action potentials, bAPs, will not be discussed here because they are not initiated in the dendrite). Other spikes, referred to as synaptic spikes hereafter, are initiated directly at the synapse and rely on ligand-gated ion channels. N-Methyl-Daspartate (NMDA) spikes, plateau potentials, and NMDA Receptor (NMDAR)-dependent Ca2+ spikes are examples of synaptic spikes. Although we focus on dendritic spikes in the neocortex and hippocampus, it is worth noting that they can be found in many other brain regions, including the striatum and amygdala, NMDA spi-

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Received: 2-July-2022, Manuscript No. PULJCPN-22-5195; Editor assigned: 04- July -2022, Pre QC No. PULJCPN-22-5195 (PQ); Reviewed: 19- July -2022, QC No. PULJCPN-22-5195 (Q); Revised: 23- July -2022, Manuscript No. PULJCPN-22-5195 (R); Published: 30- July -2022, DOI: 10.37532/puljcpn.2022.5(4).41-2.

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-kes in thalamocortical neurons, calcium spikes in granule cells of the olfactory bulb, sodium spikes in retinal ganglion cells, and LTSs in thalamocortical relay neurons. Spikes typically involve more ion channel classes than their name suggests. Nonetheless, the name of the spike is usually a good indicator of the main operating channels or initiation mechanism. Because there is no consensus on nomenclature, we focused on dendritic spikes, as they are commonly referred to in the literature. We wanted to provide a comprehensive and up-to-date summary of all known dendritic spikes recorded in the mammalian cortex, so we looked at Na+ spikes/spikelets, Ca2+ spikes, low-threshold spikes, Ca2+ plateau potentials, NMDA spikes, plateau potentials, and NMDA Receptor (NMDAR)-dependent Ca2+ spikes. An accurate picture of dendritic integration and computation must include the fine details of the various dendritic spikes described here, as well as their interactions. Ca2+ imaging, particularly in the behaving animal, has played an important role in advancing the field of dendritic computation to where it is today. Ca2+ imaging obscures the precise sub- and supra-threshold dendritic activity accessible only through electrical recordings, despite the fact that Ca2+ transients are a proxy for membrane potential.

Cortical neuron diversity is remarkable, with at least 207 subtypes estimated in the rodent somatosensory cortex. Dendritic spikes with different properties, like other cellular properties, are likely to be associated with specific neuron subtypes. For example, the excitatory neurons of L5 are traditionally divided into two types: Intratelencephalic (IT) slender tufted neurons and thick tufted Pyramidal Tract (PT) neurons. Different spatial and temporal input patterns impinge on the dendrites of PT and IT neurons. By optogenetically evoking dendritic Ca2+ currents in PT neurons of the mouse barrel cortex, the author improved perception of weak (nearthreshold) whisker stimuli in mice. Even with a limited understanding of dendritic integration, it is clear that firing a variety of spikes in multiple dendritic branches increases the computational power of the neurons. Deep artificial neural networks and, to a lesser extent, single point neurons can mimic dendrite integration and computation. Furthermore, the plasticity and modulation of dendritic and synaptic spikes themselves add another layer of complexity that may necessitate new theoretical concepts. It's unclear why evolution favors computationally (and thus biologically) complex neurons over simple elements like those found in artificial neural networks.