

# Direct recording of signal integration at individual synapses on dendritic spines: a voltage imaging study

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Most of the excitatory synapses that mediate cell-to-cell communication in the mammalian brain are located on dendritic spines. A sophisticated assembly of transmitter receptor and voltage-sensitive ion channel molecules in spines generate electrical signals and mediate plasticity in response to quantal release of chemical transmitters caused by patterned activity in presynaptic axons. Even though spines are widely considered the elementary computational units of the brain, the current understanding of their electrical behaviour is incomplete and controversial. An important question that has not been fully answered is the exact contribution of individual synapses on spines to the electrical signalling in neurons. The first step in this process involves the transfer of excitatory postsynaptic potentials (EPSPs) from the spine head, across the spine neck, to the parent dendrite at the base of the spine. The properties of this transfer define the electrical role of spines, which is currently controversial. Both old and recent results of a number of studies have been interpreted to support the prominent electrical role of dendritic spines. Other studies provided strong evidence that spines have no electrical role. None of these studies is universally accepted as conclusive because most of the available evidence is based on indirect measurements and theoretical considerations. We recently reported electrical signalling in individual spines based on voltage sensitive dye recordings. In basal dendrites of one class of cortical neurons, Layer 5 pyramidal cells, we obtained direct evidence supporting a conclusion that excitatory postsynaptic potentials (EPSPs) propagate from the synapse on spine head to the parent dendrites without voltage loss. This result implies that spines do not serve a significant electrical role. We report here a continuation of this study that includes two additional classes of principal cortical neurons and additional control experiments. The results confirm and strengthen our previous conclusion that spine synapses on basal dendrites of investigated principal neurons are not electrically isolated from the dendrites and do not function as isolated electrical compartments. Furthermore, because many presynaptic neurons fire in bursts, an important question regarding the contribution of single spine synapses to electrical signalling is the mechanism of temporal summation of subthreshold signals. We investigated this question by monitoring synaptic integration optically at the site of origin and electrically at the soma by patch pipette recording. We found that both local and somatic responses to repetitive quantal EPSPs are based almost entirely on AMPA receptor currents and strictly limited in amplitude and waveform by AMPA receptor desensitization.