Pitfalls in the interpretation of multielectrode data: on the infeasibility of the neuronal current-source monopoles

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TO THE EDITOR: Riera et al. (2012) recently presented a comprehensive multielectrode study of the barrel field of anesthetized rat. Notably, they reported that the estimated instantaneous current source density (CSD) from the recorded extracellular potentials does not sum to zero over the volume of the barrel column, indicating the presence of cortical current source monopoles on a mesoscopic (cell population) scale. The authors concluded that current source monopoles must be included in the interpretation of electrophysiological recordings (including EEG). Together with an accompanying commentary (Destexhe and Bedard 2012), it was further speculated that the estimated current monopoles are real, i.e., that single neurons may act as true neuronal current monopoles, and that the traditional cable equation may be invalid for describing biological neuronal phenomena.

However, these claims are in contradiction with well-established models of electrophysiology, including Hodgkin and Huxley’s mathematical description of axonal action potentials and the multicompartmental models of dendritic signal integration in neurons. In fact, the existence of current monopoles would be in direct violation of the Ampere-Maxwell’s law for macroscopic media (Griffiths 1999)

\[
\nabla \times \mathbf{H} = \mathbf{J}_f + \frac{\partial \mathbf{D}}{\partial t}
\]

which relates the magnetic field \( \mathbf{H} \) to the electric current density of free charges \( \mathbf{J}_f \) and the change in the displacement field \( \mathbf{D} \). By applying the divergence operator to this equation, and noting that the divergence of a curl is zero, it follows that

\[
\nabla \cdot (\mathbf{J}_f + \mathbf{J}_d) = 0
\]

where

\[
\mathbf{J}_d = \frac{\partial \mathbf{D}}{\partial t}
\]

is the displacement current. Application of the divergence theorem to Eq. 2 yields

\[
\int_V \nabla \cdot (\mathbf{J}_f + \mathbf{J}_d) dV = \int_S (\mathbf{J}_f + \mathbf{J}_d) \cdot d\mathbf{S} = 0.
\]

That is, the surface integral of the total current density must sum to zero across any arbitrary surface \( S \). This total current includes both the current from free charges \( \mathbf{J}_f \) (conductive, diffusive, and convective) and the displacement current

\[
\mathbf{J}_d = \frac{\partial \mathbf{D}}{\partial t} = \varepsilon_0 \frac{\partial \mathbf{E}}{\partial t} + \frac{\partial \mathbf{P}}{\partial t}
\]

arising from changes in the electric field \( \mathbf{E} \) and polarization \( \mathbf{P} \) (Griffiths 1999). The latter is manifested as capacitive current across the cell membrane, but in the extracellular medium it is typically insignificant compared with the current from free charges (Plonsey and Heppner 1967). Thus, irrespective of the biophysical nature of the currents (e.g., conductive, diffusive, displacement) or medium properties (e.g., inhomogeneity, isotropy, frequency dependence), the total current across an arbitrary surface always sums to zero at each time instance. As this applies to any surface, including a surface tightly encapsulating a neuron (containing also the capacitive charges attached to both sides of the cellular membrane), it follows that true neuronal current monopoles cannot exist.

Rather than interpreting Riera et al.’s (2012) estimates of the nonzero sum of CSD over the volume of interest as evidence for a violation of Maxwell’s equations, we believe a more parsimonious explanation of their estimates is either 1) the partial inclusion of the cell membrane within the volume of interest; or 2) a violation of some of the assumptions inherent in the particular CSD estimation methods used (Pettersen et al. 2006). Generally, a volume enclosed by a surface \( S \) and corresponding to the cortical column will not include the membrane of entire cells, especially that of distal dendrites and the axons projecting outside of the local column. Applying Eq. 4 to each cell enclosed by \( S \) yields that the sum of the intracellular currents out of \( S \) equals the negative sum of transmembrane currents within \( S \). Consequently, the sum of CSD over the volume will be truly nonzero whenever the bounding surface crosses the membrane of active cells. Furthermore, since both of the CSD techniques used by Riera et al. (2012) rely on assumptions regarding the lateral distribution of neuronal activity, the extracellular conductivity, and the detailed positions of the electrode contacts, the resulting estimates are likely to be biased due to violations of some of those assumptions.

DISCLOSURES

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