Reply to Gratiy et al.

Jorge Riera¹ and Alejandro Cabo²

¹Department of Biomedical Engineering, Florida International University, Miami, Florida; and ²The Institute of Cybernetics and Mathematics Applied to Physics (ICIMAF), Havana, Cuba

INSTANTANEOUS CHARGE UNBALANCE IN THE BRAIN: A RESULT FROM PROCEDURAL ERRORS OR AN AUTHENTIC PHYSICAL PHENOMENON?

TO THE EDITOR: Gratiy et al. (2013) proposed two alternative explanations for the nonbalanced current source density (CSD) estimates in Riera et al. (2012). Their commentary was based on a particular interpretation of the role played by the Ampere-Maxwell Law in the genesis of the electric fields for macroscopic media. In this Reply, we will provide further information to stimulate the debate in the community.

Plausible Procedural Errors

We believe that partial inclusion of the cell membrane is not a conceivable situation in the particular case of CSD volumetric distributions of back-propagating action potentials. Riera et al. (2012) carefully selected spiking neurons (i.e., pyramidal and spine stellate cells) with somas around the center of the 3D probe. Based on the morphology of these neurons (Elston and Rosa 1998; Romand et al. 2011; Staiger et al. 2004), it is unlikely that significant parts of their dendrites were outside the region covered by the probe. In addition, it is well known that the amplitude of back-propagating action potentials, and consequently of the associated transmembrane currents, tends to decay rapidly from the soma to the dendrites, with experimental (Bar-Yehuda et al. 2008; Gulledge and Stuart 2003) and theoretical (Wang et al. 2013) estimations available for pyramidal cells. As discussed by Riera et al. (2012), vessels and axons in the neocortex could have caused a shunting of electric currents to remote locations and hence could have brought about an apparent unbalance in the estimated current sources.

For the analysis of volumetric extracellular potentials, the authors employed a method that does not make assumptions on the lateral distributions of neuronal activity (Goto et al. 2011) and used accurate values of the extracellular conductivity and electrode positions (Goto et al. 2010). Using simulations, we demonstrated that such a CSD method does not introduce charge imbalances (data not shown, unpublished observations). However, methods for CSD analysis were all based on the validity of quasi-stationarity of the Maxwell equations. We would expect strong bias in the estimated CSD distributions if this approach were no longer valid (Wang et al. 2013). Finally, extracellular electrical potentials were recorded using filters with cut-off frequency larger than 8 kHz. Riera et al. (2012) provided an explanation for the CSD unbalance based on both sampling limitations and particular characteristics of brain tissues (i.e., anisotropy and inhomogeneity). In any of the cases discussed above, modeling and methods used today to interpret CSD distributions must be revisited as a consequence of the experimental data presented by Riera et al. (2012).

An Authentic Physical Phenomenon

The question of this debate is whether or not the net electric charge crossing an imaginary closed surface at any time instant needs to be necessarily zero. The answer to this question is not in the Ampere-Maxwell Law, but in the charge continuity principle, which also comprises the Poisson’s Law:

\[ \nabla \cdot \mathbf{j}_T + \frac{\partial \rho_f}{\partial t} = 0 \]

\[ \mathbf{j}_T = \mathbf{j}_M + \mathbf{j}_D \]

It states that if there are variations in the total charge inside any imaginary surface, then the total electric current (e.g., migration \( \mathbf{j}_M \), diffusion \( \mathbf{j}_D \)) across its surface will be not null. Then, the problem is reduced to determine whether or not a charge can be temporally retained inside that imaginary surface before it is screened by the medium. In the frequency range of electrophysiological recordings, mean values for the electric conductivity and permittivity are \( \sigma = 0.28 \ \text{S/m} \) (Goto et al. 2010) and \( \varepsilon = 5 \times 10^6 \varepsilon_0 \) (Gabriel et al. 1996), respectively. Assuming that extracellular ionic contributions are predominant at this macroscopic level, and that, as a first approach, the tissue could be considered homogeneous, then the ionic strength will be \( I = 150 \ \text{mM} \). Therefore, the decay time constant \( \tau = \varepsilon/\sigma \) and the Debye length \( R_D = \sqrt{\varepsilon RT/2F^2 I} \) will not be small enough (i.e., \( \tau = 0.16 \ \text{ms} \) and \( R_D = 0.21 \ \mu \text{m} \)) as to assume a perfect electric field screening out at this particular scale. The decay time constant determines the volatility of any free electric charge (\( \rho_f(t) \)) in the medium \( \rho(t) = \rho_f(t)e^{-t/\tau} \) and the Debye length determines the shielding of the electric field \( \varphi(r) = \frac{\rho_f(t)}{4\pi \varepsilon_0 R_D} e^{-r/R_D} \) produced by such a charge. Alternatively, assuming that the screening is instantaneous and that the “s” variable is nonvanishing outside the membrane, it follows that a monopole for it will be exactly canceled by the also nonvanishing monopole of the assumed volumetric ohmic currents.

DISCLOSURES

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¹ We assumed that there is no convection current, i.e., \( \mathbf{j}_C = 0 \)
AUTHOR CONTRIBUTIONS

J.J.R. and A.C. conception and design of research; J.J.R. drafted manuscript.

REFERENCES


